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The Mammalian Faunas of the Washakie Formation, Eocene Age, of Southern Wyoming. Part III. The Perissodactyls

Steven M. McCarroll
John J. Flynn
William D. Turnbull

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Steven M. McCarroll
John J. Flynn
William D. Turnbull

Department of Geology
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605-2496

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The Mammalian Faunas of the Washakie Formation, Eocene Age, of Southern Wyoming. Part III. The Perissodactyls

Steven M. McCarroll **John J. Flynn** **William D. Turnbull**

Abstract

Eighteen perissodactyl taxa have been identified in the Field Museum collections from the Washakie Formation, Washakie Basin, Wyoming: *Orohippus* sp., *Epihippus gracilis, Telmatherium* sp., *Mesatirhinus* sp., *Metarhinus* sp., *Dolichorhinus* sp., Brontotherioidea indeterminate, *Isectolophus latidens, Eomoropus amarorum, Helaletes nanus, Dilophodon minusculus, Hyrachyus modestus, Hyrachyus eximius, Triplopus cubitalis, Triplopus implicatus,* cf. *Forstercooperia minuta,* Hyracodontidae indeterminate, and *Amynodon advenus.* At present, the Washakie Formation is divided into two members: the lower Kinney Rim Member and the upper Adobe Town Member. The Adobe Town Member is informally divided into lower, middle, and upper units, with the Bridgerian–Uintan North American Land Mammal "Age" boundary currently placed between the lower and middle units.

The Kinney Rim Member contains *Mesatirhinus* sp., *Helaletes nanus, Hyrachyus modestus,* and *Hyrachyus eximius. Helaletes nanus* and *Hyrachyus modestus* occur throughout the Bridgerian, and their usefulness in defining finer temporal divisions is thus limited. *Hyrachyus eximius* elsewhere is limited in age to the late Bridgerian. Its occurrence near the base of the Kinney Rim Member indicates the lack of early Bridgerian age sediments in the Washakie Formation. *Telmatherium* sp., *Mesatirhinus* sp., *Isectolophus latidens, Hyrachyus modestus,* and *Hyrachyus eximius* are present in the lower unit of the Adobe Town Member, also considered to be late Bridgerian in age. *Metarhinus* sp., *Dolichorhinus* sp., *Eomoropus amarorum, Dilophodon minusculus, Triplopus cubitalis, Triplopus implicatus,* cf. *Forstercooperia minuta,* and *Amynodon advenus* occur only in the middle unit of the Adobe Town Member. All these taxa have early Uintan first occurrences except *Dilophodon minusculus* and *Hyrachyus eximius,* which have late Bridgerian first occurrences, and *Amynodon advenus,* which has an earliest Uintan first occurrence. Additionally, *Dilophodon minusculus* and *Hyrachyus eximius* are known from earliest Uintan deposits elsewhere. This apparent overlap of late Bridgerian taxa with early Uintan taxa in the middle unit of the Adobe Town Member indicates that the Shoshonian Subage of the Uintan North American Land Mammal "Age" may be present within the middle unit of the Adobe Town Member in addition to the lower unit, as previously suggested by Flynn (1986). The presence of the Uintan taxon *Epihippus gracilis* from the upper unit of the Adobe Town Member indicates only an undifferentiated Uintan age. Among perissodactyls, the future discovery of *Colodon* or *Epitriplopus* (both late Uintan first appearance taxa) from the upper unit of the Adobe Town Member would indicate the presence of the early–late Uintan boundary within the Washakie Formation.

Introduction

The Washakie Formation consists of fluvial rocks of Eocene age cropping out in the Washakie Basin of southwestern Wyoming and the Sand Wash Basin of northwestern Colorado (Roehler, 1973). This paper deals only with the Washakie Formation within the Washakie Basin as defined by the Rock Springs uplift to the west, the Cherokee Ridge to the south, the Sierra Madre uplift to the east, and

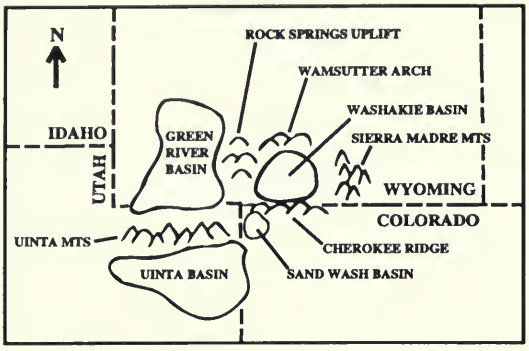

FIG. 1. General location map showing geographic relationship of the Washakie, Green River (containing the Bridger Basin), and Uinta basins (from Roehler, 1973).

the Wamsutter arch to the north (Fig. 1). Correlation of the Washakie Formation between the Sand Wash Basin and the Washakie Basin, however, is discussed briefly. Within the Washakie Basin (Fig. 2) the Washakie Formation crops out in an area of about 680 square miles in the geographic center of the basin (Roehler, 1973).

Granger (1909) divided the Washakie Formation into two lithostratigraphic units, the lower Washakie A and the upper Washakie B. Washakie A corresponded faunally with faunas from the Bridger C–D, and Washakie B corresponded faunally with faunas from the Uinta A–B. As later defined by Roehler (1973), the Washakie Formation is divided into two members, the lower Kinney Rim Member (~900 ft/270 m thick) and the upper Adobe Town Member (~2,300 ft/700 m thick). In addition, the Adobe Town Member is divided into three informal units: lower, middle, and upper (Fig. 3). Granger's Washakie A is equivalent to Roehler's lower unit of the Adobe Town Member, and Granger's Washakie B is equivalent to Roehler's middle unit of the Adobe Town Member. The Kinney Rim Member of Roehler's section was considered to be the uppermost part of the Green River Formation by Granger (1909). Granger did not recognize rocks stratigraphically higher than those capping Haystack Mountain, but subsequent work by Roehler (1973) and Turnbull (1972) showed a sequence of beds near the geographic center of the basin to be stratigraphically higher than the top of Haystack Mountain; the uppermost of these rocks are the upper unit of the Adobe Town Member.

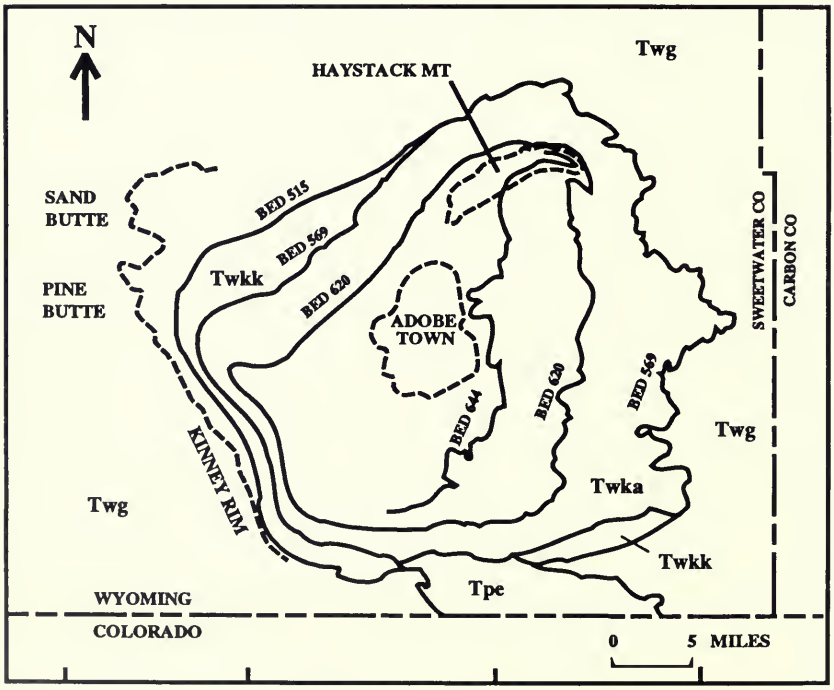

FIG. 2. Detailed map of study area showing outcrop extent of the Washakie Formation members and informal units. Major physiographic features are also shown. Abbreviations as follows: Twg = Wasatch and Green River formations; Twkk = Washakie Formation, Kinney Rim Member; Twka = Washakie Formation, Adobe Town Member; Tpe = post-Eocene rocks (from Roehler, 1973).

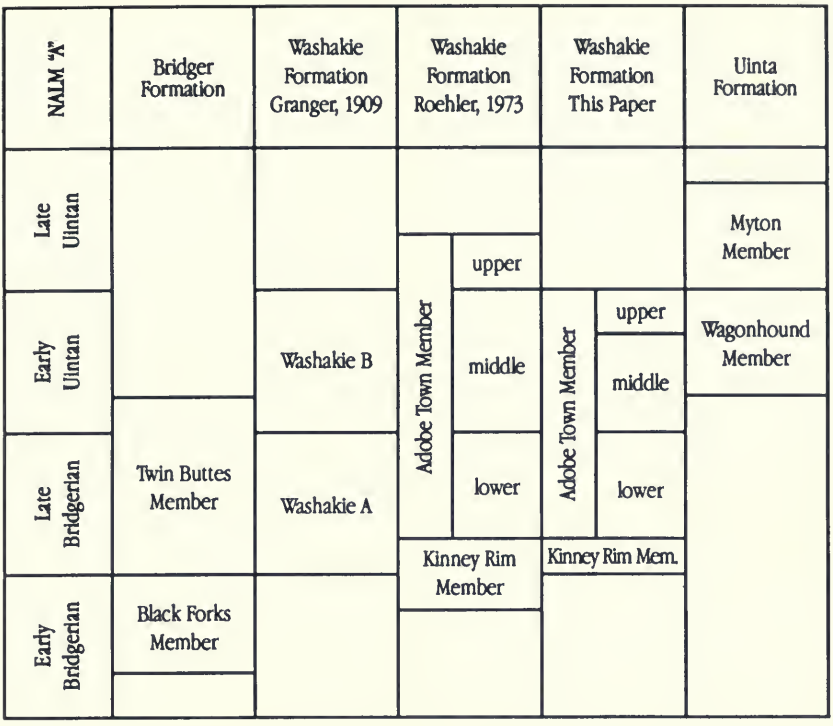

FIG. 3. Generalized correlation of the Washakie, Bridger, and Uinta formations to the North American Land Mammal Ages. The upper Bridger Formation is shown to include earliest Uintan time, based on the biostratigraphic results of Evanoff et al. (1994) and the stratigraphic correlations of Roehler (1992).

Roehler (1973) speculated that some lower portion of the Kinney Rim Member was early Bridgerian in age and that the upper unit of the Adobe Town Member was possibly late Uintan in age. These age assignments were tentative, based on lithostratigraphic changes, and have not been borne out by subsequent faunal evidence. Recently, McCarroll et al. (1993, 1996) have shown that no definitive faunal evidence supports an early Bridgerian age for the Kinney Rim Member, and it should be considered late Bridgerian in age (although to date, no specimens have come from the lowest 30 m of this member). In addition, no definitive faunal evidence supports a late Uintan age for the upper unit of the Adobe Town Member, and it should be considered early Uintan in age.

Fossil vertebrates were first collected from the Washakie Formation in the 1870s (for complete histories see Roehler, 1973, and Turnbull, 1978). Fossil mammals are found throughout the formation but are rare in the Kinney Rim Member and very rare in the upper unit of the Adobe Town Member. No comprehensive faunal revisions of the Washakie Formation faunas have been produced, as has been the case for other western North American faunas (for example, the lower Eocene Wasatch and Wind River faunal revisions of Matthew & Granger, 1915). Even so, selected Washakie Formation taxa have been included in various taxonomic descriptions and revisions, or taphonomic reports (Osborn, 1929, titanotheres; Wheeler, 1961, uintatheres; Radinsky, 1967a, Hyracodontidae; Turnbull & Martill, 1988, *Mesatirhinus* [= *Metarhinus* of this paper]; Turnbull, 1991, *Protoptychus*).

Collection efforts by the Field Museum in the Washakie Formation were begun in the late 1940s by Rainer Zangerl. Zangerl's main interest was the collection of the varied reptilian fauna. One of Zangerl's field assistants was William D. Turnbull, who is now Curator Emeritus at FMNH. Over the past four decades (although not every year) Turnbull has made an extensive collection of the mammalian fauna (Turnbull, 1972). This report concentrates on specimens in the FMNH collections (and a few from CM) and is not an inclusive report of all Washakie Formation perissodactyl specimens in other collections (see Turnbull, 1978, for a discussion of Washakie Formation collections in other institutions). In addition, many of the

more complete titanothere specimens are still not identifiable to genus, as they do not preserve diagnostic characters. These and unidentifiable postcranial specimens are not included in this study. Such exclusions explain the small number of specimens in this study, although fossils are much rarer in the Washakie Formation than in the Bridger Formation. For our purposes, the most important of the older FMNH collections are:

1) A small but very important fauna from the Kinney Rim Member. Roehler (1973) recognized the Kinney Rim Member as distinct from the underlying Green River Formation, and more characteristic of, and assignable to, the Washakie Formation. Prior to Turnbull's collecting, no fossils were known from the section of rocks now placed within the Kinney Rim Member.
2) The rim below the Adobe Town Rim. Within this set of beds, Flynn (1986) postulated the presence of the Shoshonian Subage (earliest Uintan) of the Uintan North American Land Mammal "Age" (NALMA) within the Washakie Formation. ("Age" is in quotation marks because the NALMAs are not based on corresponding time stratigraphic stages.)
3) Haystack Mountain. Many of the classic Uintan age collections from the Washakie Formation were made from Haystack Mountain (Mammoth Buttes of Cope). Cope (1884) distinguished Haystack Mountain as the eastern tip of the Mammoth Buttes; subsequent usage refers to this entire linear feature (see Fig. 2) as Haystack Mountain (Turnbull, 1978, p. 581). In addition to these three major efforts, Turnbull has collected throughout the basin and from within the entire stratigraphic section.

More recent Field Museum collecting efforts began in the summer of 1990, under the direction of John J. Flynn and William D. Turnbull, and continue to the present. As with the earlier efforts, reconnaissance collecting has encompassed the entire stratigraphic section and much of the areal extent of the Washakie Formation. Concentrated collection efforts have been made in the southern and southeastern portions of the basin (areas undercollected historically, Turnbull, 1972). Of particular interest is a series of red beds (the middle red beds of Roehler, 1973) that have produced a fauna rich in smaller taxa (insectivores, primates, rodents, creodonts) but few perissodactyls to date. Stratigraphically, these red beds are approximately equivalent to the less fossiliferous beds of the rim below the Adobe Town Rim, which is exposed in the northwestern portion of the basin, and the Willow Creek Rim, which is exposed in the northeastern part of the basin. Also of note is a small mammalian fauna from the upper unit of the Adobe Town Member that at present indicates an early Uintan age for the upper unit. This fauna will be reported elsewhere (McCarroll, 1995, in prep.).

The Washakie Formation is important because of its well-preserved fossil fauna and the presence of the Bridgerian–Uintan NALMA boundary within the formation. When fossils were first discovered in western North America, the larger and most productive basins were heavily collected and many of the NALMAs were a direct result of this early work. As we understand more about the NALMAs, it becomes imperative that we also try to tie them together so that the transitions and boundaries between them can be documented, defined, and dated. A recent example of this kind of work is Flynn's (1986) assessment of the Bridgerian–Uintan transition in western North America. Flynn (1986) used biostratigraphy, magnetic polarity stratigraphy, and radioisotopic dating to correlate the Bridgerian–Uintan transition between the Washakie Formation, the Aycross and Tepee Trail formations of northwestern Wyoming, and the marine and continental La Jolla and Poway groups of southern California. Flynn (1986) named the Shoshonian (earliest Uintan) a subage of the Uintan NALMA. The Shoshonian was defined (see Flynn, 1986, p. 380) by the first appearance of *Amynodon* and characterized by the co-occurrence of what previously had been regarded as typically late Bridgerian or early Uintan taxa. These taxa tended to be (but were not exclusively) smaller-bodied Bridgerian taxa (i.e., *Hyopsodus,* primates, rodents) and larger-bodied Uintan taxa (i.e., perissodactyls).

The Uintan NALMA has gone through many changes since its inception (summarized in Krishtalka et al., 1987). Herein, we recognize three biochronologic divisions of the Uintan NALMA: 1) the earliest Uintan or Shoshonian, 2) the early Uintan, and 3) the late Uintan. At present, there is no known fauna from the Uinta A lithostratigraphic unit of the Uinta Basin, and the age of Uinta A strata relative to the Shoshonian and other Uintan temporal subdivisions is not well understood. A portion (or all) of the Uintá A strata may be time equivalent to the earliest Uintan. The Bridgerian NALMA, by contrast, has had a fairly

straightforward history (Krishtalka et al., 1987). The Bridgerian is divided into three biochronologic divisions: 1) earliest Bridgerian or Gardnerbuttean, 2) early Bridgerian, and 3) late Bridgerian. Historically, the Washakie Formation has been temporally correlated with varying portions of the Bridger and Uinta formations (see Fig. 3).

In this paper and a previously published abstract (McCarroll, 1994) we concentrate on the perissodactyls for the following reasons, all of which relate to the biostratigraphic and biochronologic usefulness of the perissodactyls:

1) The stratigraphic distribution of perissodactyls is fairly even throughout the formation. Primates are much more common finds (abundance) in any particular field season, but their distribution within the formation is limited to one or two productive layers within the lower unit of the Adobe Town Member.
2) The taxonomic diversity of perissodactyls is relatively high. To date, we have recovered 18 perissodactyl taxa from the Washakie Formation. To use primates as an example once again, we find only four genera and four species of primates known to date.
3) Taxonomic revisions of the perissodactyls have been fairly numerous, resulting in elucidation of the combination of primitive and derived characters by which these taxa can be recognized. Unfortunately, in this respect some specimens reported here can only tentatively be assigned to a taxon, as they do not preserve some of the defining characters. In addition, revisions are needed for some perissodactyl groups (see Schoch, 1989). The present paper is not a systematic revision. Even so, we discuss problems involving perissodactyl systematics, specifically morphological characters used to define taxa.

Abbreviations and Institutions

L indicates length; W, width. Bed numbers are those of Roehler (1973) (or Granger, 1909, as noted). Many specimens are not given specific bed numbers because of the difficulty of determining exactly which bed a specimen was collected from; most of the beds numbered by Roehler (1973) are not laterally continuous. Molarization terminology is that of Radinsky (1967a). Cusp terminology is that of Hooker (1989, Fig. 1). Detailed locality information for locality abbreviations cited in the text is given in Appendix 1 (except those listed in Turnbull, 1978). All specimen measurements are in millimeters (mm). AMNH = American Museum of Natural History, CM = Carnegie Museum of Natural History, FMNH or FM = Field Museum of Natural History, JJF = John J. Flynn, NALMA = North American Land Mammal Age, PM or P = FMNH fossil mammal collection, UCMP = University of California Museum of Paleontology, Berkeley, UW = The Geological Museum, The University of Wyoming, WDT or KLWDT = William D. Turnbull or Kubet Luchterhand, YPM = Yale Peabody Museum, YPM-PU = Princeton University (now housed at the Peabody Museum of Natural History, Yale University).

Systematic Paleontology

Order Perissodactyla Owen, 1848
Infraorder Hippomorpha Wood, 1927
Superfamily Equoidea Grey, 1821
Family Equidae Grey, 1821

***Orohippus* sp. Marsh, 1872**
(Fig. 4A)

REFERRED SPECIMENS—PM 55790, isolated left M^1, from Loc. JJF 7-26-92-1, $Twka_1$; PM 39944, paired lower jaws with partial right and left M_3 from Loc. FM-6-83-KLWDT, $Twka_1$.

DESCRIPTION—PM 55790 (Fig. 4A) is an almost complete left M^1 lacking only the parastyle. It appears to be an M^1 rather than an M^2 because of its square outline and a hypocone that is slightly more prominent than the protocone. If PM 55790 were a P^4, one would expect a more prominent protocone and a smaller hypocone. A small mesostyle is present. Small but distinct paraconule and metaconule are present, which may appear larger in less worn specimens of the same size and taxon.

DISCUSSION—Granger (1908) differentiated *Orohippus* from *Hyracotherium* (= *Eohippus*) by the progressive molarization of the premolars in *Orohippus*. He recognized 10 species of *Orohippus*. More recently, Kitts (1957) revised the genus and recognized only five species.

Compared to the measurements reported by Kitts (1957) for *Orohippus*, PM 55790 (see Table 3) is outside the size ranges of the much larger *O.*

major and *O. agilis*; it is within the size range of *O. pumilus*. It is slightly smaller than measurements reported for *O. progressus* and *O. sylvaticus*, although only one M^1 measurement was reported for *O. progressus* by Kitts (1957). PM 55790 may represent a small individual of *O. sylvaticus*, as it is morphologically indistinguishable from YPM 11322, a specimen of *O. sylvaticus* preserving P^2–M^1 figured by Kitts (1957, Fig. 8A,B). As stated previously, PM 55790 is also within the size range of *O. pumilus*, a taxon previously known only from Bridger B beds of the Bridger Formation (Kitts, 1957).

PM 55790 is from the rim below the Adobe Town Rim that is thought, based on other taxa (Granger, 1909), to be late Bridgerian in age. At present, the limited Washakie material assignable to *Orohippus* prevents a definitive species-level identification. At present, taxa restricted to the Bridger B beds of the Bridger Formation are unknown from the Washakie Formation. If future specimens indicate the undisputed presence of *O. pumilus* from the rim below the Adobe Town Rim, either the temporal range of *O. pumilus* should be revised to include the late Bridgerian or, less likely, given current knowledge of the temporal distribution of taxa, the age of a portion of the lower unit of the Adobe Town Member may be older (early Bridgerian) than presently recognized (late Bridgerian).

***Epihippus gracilis* (Marsh, 1871)**
(Fig. 4B,C)

REFERRED SPECIMEN—PM 55311, left dentary with dP_1–M_2 with the unerupted M_3 exposed in the lingual surface of the dentary, from Loc. JJF 7-21-90-1, $Twka_3$.

DESCRIPTION—PM 55311 (Fig. 4B,C) possesses a diastema between the canine alveolus and the root of dP_1. Two foramina are present on the labial surface of the dentary. The larger anterior mental foramen is under the diastema and the smaller posterior mental foramen is directly under dP_2.

PM 55311 is missing dP_1, which appears to be single-rooted. dP_2 possesses a metaconid–metastylid complex; this area is too worn to determine with certainty if the metaconid and metastylid were distinct, but a small posterior extension of enamel from this area leads us to think that they were. The protoconid is small and the paracristid and protocristid are not well developed. The cristid obliqua is complete, intersecting the posterolabial base of the metaconid–metastylid complex. The hypoconid is well developed with a hypolophid connecting it to a very small entoconid. A small postcristid branch extends posteriorly from the small entoconid. The postcristid branch appears to be notched, separated from the main body of the tooth by a wear facet. Distinct cingula are not present.

dP_3 and dP_4 are more molarized than dP_2, with better developed protocristid and paracristid; the paracristid descends anterolingually from the protoconid and bends sharply lingually near the midline of the tooth. This pattern is repeated in the remaining, more posterior teeth. The entoconid on dP_3 and dP_4 is better developed than that of the dP_2, appearing as a distinct cusp. The protocristid branch is also more distinct and located more medially but is still slightly linguad of the tooth midline. The metaconid and metastylid are distinct cusps; the metaconid on dP_3 is at the midline of the tooth but more linguad on dP_4 than on dP_3. Small anterior, posterior, and lingual cingula are present on dP_3 and they are slightly larger on dP_4.

M_1 and M_2 are distinctly more squared than the deciduous premolars, which are narrower anteriorly, giving them a trapezoidal outline. As on DP_{3-4}, the area between the postcristid branch and the posterior edge of the entoconid forms a small anteroposteriorly oriented groove, slightly lingual to the midline of the tooth. Well-developed cingula are present on both M_1 and M_2, although they are slightly reduced labially on M_2.

DISCUSSION—Granger (1908) recognized only two species of *Epihippus: E. gracilis* and *E. parvus*. He distinguished *E. parvus* from *E. gracilis* by its smaller size, greater development of the parastyle, and its compressed mesostyle. Granger (1908) did not recognize *E. uintensis* (= *Orohippus uintensis*) and considered it synonymous with *E. gracilis*.

MacFadden (1980), in a study of the perissodactyls of the Tepee Trail Formation of northwestern Wyoming, recognized both *E. gracilis* and *E. uintensis*, differentiating the two solely on the basis of size. MacFadden (1980) found no morphologic or size differences between *E. parvus* and *E. gracilis* and considered *E. parvus* to be synonymous with *E. gracilis*. Length–width plots for *Epihippus* P_4's (see MacFadden, 1980, Fig. 3) show two discrete size populations, the larger *E. uintensis* and the smaller *E. gracilis*. The more important measure for distinguishing the species is tooth width, as the P_4 lengths for the two species overlap.

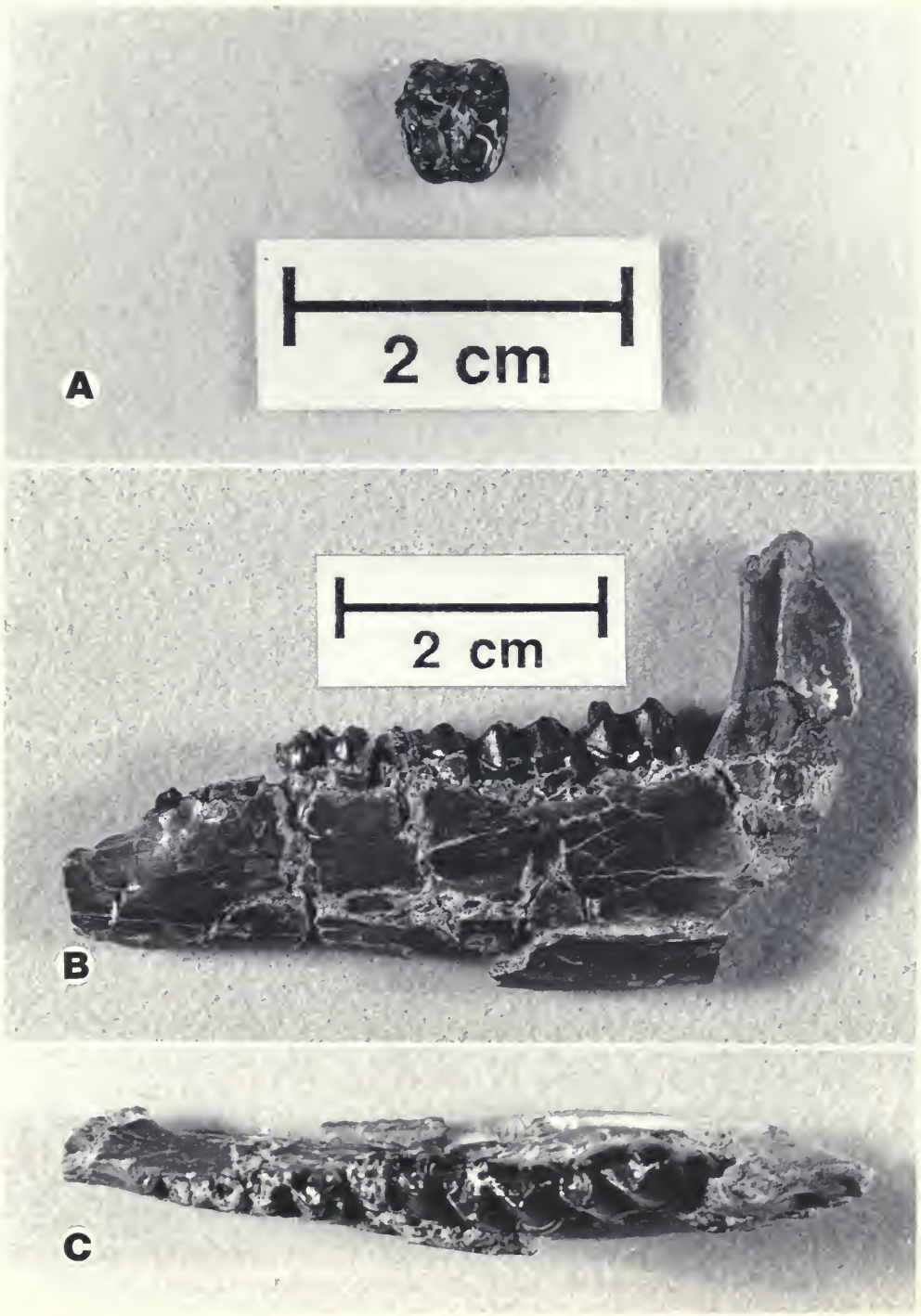

FIG. 4. **A,** *Orohippus* sp., PM 55790, isolated left M^1, in occlusal view (FMNH neg. 85813). **B–C,** *Epihippus gracilis,* PM 55311, left dentary with dP_1–M_2. **B,** Lateral view (FMNH neg. 85824.27). **C,** Occlusal view (FMNH neg. 85825.6).

PM 55311 is confidently assigned to *Epihippus* based on the degree of loph development of the molars, which is typical for *Epihippus*. PM 55311 is too small to be *E. uintensis*, and is assigned to *E. gracilis* solely on the basis of size (see Table 2).

PM 55311 is from the upper unit of the Adobe Town Member, a unit that produces few mammal fossils. *Epihippus gracilis* is currently known from throughout the entire Uintan elsewhere, and its occurrence here indicates a Uintan age assignment for the upper unit.

Infraorder Titanotheriomorpha Hooker, 1989
Superfamily Brontotherioidea Marsh, 1873

Our discussion of the Washakie Formation titanotheres will be limited to the generic level. A good generic-level revision of the group has recently been published (Mader, 1989). That revision included generic diagnoses based on numerous primitive and derived characters, allowing us to confidently identify the specimens in this study. We consider only taxa represented by complete or partial skulls for this titanothere section, because many of the taxa are indistinguishable on the basis of dentition and because Mader's (1989) revision showed most of the diagnostic derived, generic characters to be cranial. The species-level taxonomy of titanotheres is still in need of extensive and thorough revision, and we therefore will not attempt species-level identifications. All dental measurements of titanothere specimens are given in the respective taxic descriptions rather than in a separate table; following Mader (1989), only P^2–M^3 measurements are presented.

Telmatherium sp. Marsh, 1872

REFERRED SPECIMEN—PM 56049, almost complete skull (partially prepared), from Loc. JJF 8-11-93-1, $Twka_1$.

DESCRIPTION—PM 56049 is a large titanothere with a P^2–M^3 length greater than 160 mm. The unprepared nature of the specimen prevents an accurate P^2–M^3 measurement at this time. The sagittal crest is well developed.

DISCUSSION—PM 56049 is assigned to *Telmatherium* based on its size and well-developed high, narrow sagittal crest. PM 56049 is within the size range of *Dolichorhinus*. *Dolichorhinus*, however, possesses a low, broad sagittal crest (Mader, 1989).

Mesatirhinus sp. Osborn, 1908
(Figs. 5A,B, 6A,B)

REFERRED SPECIMENS—PM 27939, complete skull with upper dentition, from Loc. FM-11-70-WDT, Twkk, bed 527; PM 27938, partial juvenile skull preserving P^1, dP^{2-4}, M^{1-2}, and indication of the crypt of M^3, from Loc. FM-11-70-WDT, Twkk, bed 527; PM 36045, almost complete skull and skeleton, from Loc. FM-2-72-WDT, $Twka_1$.

DESCRIPTION—PM 27939 (Fig. 5A,B) is a medium-sized titanothere with a P^2–M^3 length of 137.0 mm. PM 27939 has a very small diastema between the canine and the P^1 alveolus. Both P^1's are missing, and P^2–P^4 are unmolarized. The orbit is only moderately developed, and a broad suborbital protuberance is present. The zygomatic arch is moderately large and curved.

The skull of PM 36045 (Fig. 6A,B) is almost complete, missing only portions of the anterior dentition, portions of the molars, and a small portion of the sagittal crest and the left frontal–nasal boundary. P^2–M^3 length is 135.2 mm. PM 36045 possesses fairly robust nasals, which are slightly flared distally. The nasal incision, which is crushed, appears to extend back to the posterior border of the M^1. The orbital area is also crushed, but appears not to have been enlarged. The suborbital protuberance is long and well developed. The right canine is present and has moved out of the alveolus by approximately ½ inch. This makes the canine appear enlarged when actually it is fairly small. Very small upper diastemas are present between the canine and the I^3 and P^1.

Mader (1989) was unable to corroborate the assertion by Osborn (1929) that *Mesatirhinus* possessed incipient horns. PM 36045 possesses what appears to be an "incipient" horn on the right side of the skull near the frontal–nasal boundary. This area is not preserved on the left side of the skull. The "incipient" horn of PM 36045 might be an artifact of crushing. Osborn often ignored deformation due to crushing, and his observation of incipient horns in specimens assigned to *Mesatirhinus* may have been a result of postdepositional deformation of certain specimens. Comparisons with other skulls, however, indicate that the incipient horns of PM 30645 are real and not an artifact of crushing.

FIG. 5. *Mesatirhinus* sp., PM 27939, complete skull. **A,** Dorsal view (FMNH neg. 85824.7). Arrow indicates large suborbital protuberance characteristic of *Mesatirhinus*. **B,** Lateral view (FMNH neg. 85824.16).

FIG. 6. *Mesatirhinus* sp., PM 36045, almost complete skull. **A,** Dorsal view (FMNH neg. 85811). Arrow 1 indicates posteriormost extension of the lateral nasal incision; arrow 2 indicates anteriormost extension of the orbit. Note that the lateral nasal incision does not reach back to the orbit, characteristic of *Mesatirhinus*. **B,** Lateral view (FMNH neg. 85812).

DISCUSSION—According to Mader (1989), *Mesatirhinus* is distinguished from *Metarhinus* by the morphology of the nasal and orbital regions. In *Mesatirhinus* the lateral nasal incision does not extend as far back as the orbital region, in contrast to the condition in *Metarhinus*. *Mesatirhinus* possesses a prominent suborbital protuberance, and the orbit is not prominent. In contrast, *Metarhinus* possesses a small suborbital protuberance and the orbit is prominent. Even though PM 36045 is dorsoventrally crushed, the orbits are clearly not pronounced. In addition, the lateral nasal incision does not extend as far posterior as the rim of the orbit.

PM 27939 is moderately crushed, affecting direct comparison with Mader's (1989) generic diagnosis of *Mesatirhinus*. Characters used by Mader (1989) that are also present in PM 27939 include small canines, very small upper diastema, unmolarized premolars, well-developed suborbital protuberance, and no hypocone on M^3. The nature of the nasals is difficult to determine because of crushing. It appears, however, that after correcting for crushing the nasals would have been flared distally.

PM 27938 and PM 27939 are from the Kinney Rim Member, and PM 36045 is from the lower unit of the Adobe Town Member. *Mesatirhinus* is currently known from the Bridgerian elsewhere (Mader, 1989).

***Metarhinus* sp. Osborn, 1908**
(Fig. 7A,B,C)

REFERRED SPECIMENS—PM 3935, anterior half of skull with right and left P^1–M^3, from Loc. FM-3-57-WDT, $Twka_2$; PM 56023, left half of skull with C–M^3, from Loc. FM-6-58-WDT, $Twka_2$. PM numbers for the skull (n = 15), lower jaw (n = 27), isolated teeth (n = 85), and postcranial specimens (n = 106) from a monospecific titanothere (*Metarhinus*) assemblage are given in Appendix 2. This assemblage has been described by Turnbull and Martill (as *Mesatirhinus*) (1988); all specimens from this quarry are from Loc. FM-12-70-WDT, $Twka_2$, bed 643 or low in bed 644. Because it is from a single catastrophic event, this assemblage provides an important record of variation within a single titanothere taxon, comparable to single locality samplings of modern animals. This is in contrast to the typical time-averaged accumulation samples of most titanothere taxa. Additional study of the paleobiology of this assemblage is planned for a future date. One specimen (PM 35932) from the quarry is figured here (Fig. 7C) to further document the generic assignment of the quarry sample.

DESCRIPTION—PM 3935 (Fig. 7A,B) is a medium-sized titanothere with a P^2–M^3 length of 144.0 mm. PM 3935 possesses a prominent orbit and a deep nasal incision that reaches back to the front of the orbital region. There is a small but obvious suborbital protuberance. The nasal region is slightly crushed and it is difficult to discern whether the nasals are constricted at the base. Although the nasals appear to be slightly constricted at the base, it is possible that if the skull were uncrushed the constriction would appear greater; alternatively, the apparent constriction now present may be a result of crushing, in which case the uncrushed skull would have no constriction.

PM 35932 (Fig. 7C) is a poorly preserved, crushed skull from the *Metarhinus* quarry. It possesses a large bony orbit, small suborbital protuberance, and a nasal incision that reaches back to the orbit. The P^2–M^3 length is 157.0 mm.

DISCUSSION—Overall, the nasals of PM 3935 are most similar to the spoon-shaped nasals of *Metarhinus* rather than the unconstricted, distally flared nasals of *Mesatirhinus* or the shorter, tapered nasals of *Rhadinorhinus*. The tips of the nasals do seem to taper slightly, giving them a distinct spoon shape; this tapering is not the same as in *Rhadinorhinus*, in which the nasals taper from their base to their tips. Of titanotheres possessing a suborbital protuberance, *Metarhinus* is the only one in which it is small; *Mesatirhinus*, *Rhadinorhinus*, and *Dolichorhinus* all possess a large suborbital protuberance. The lateral nasal incision in PM 3935 and PM 35932 extends back to the orbital region, as described for *Metarhinus* (Mader, 1989). The posterior extension of the nasal incision may in part be attributed to crushing of surrounding bones, although we think it is clear that the nasal incision reached the orbital region in this specimen. The crushing in PM 3935 is most extensive on the right side. This crushing may have displaced the lateral nasal incision further posteriorly than it actually was, on the less crushed left side; however, the lateral nasal incision still reaches the anteriormost portion of the prominent orbit.

Generic assignment of the titanothere quarry sample of Turnbull and Martill (1988) is changed from *Mesatirhinus* to *Metarhinus*. These specimens were assigned to *Mesatirhinus* prior to Mader's (1989) revision. The small suborbital protuberance, large bony orbit, and deep nasal incision all indicate *Metarhinus* rather than *Mesatirhinus*.

PM 3935, PM 56023, and the quarry sample are

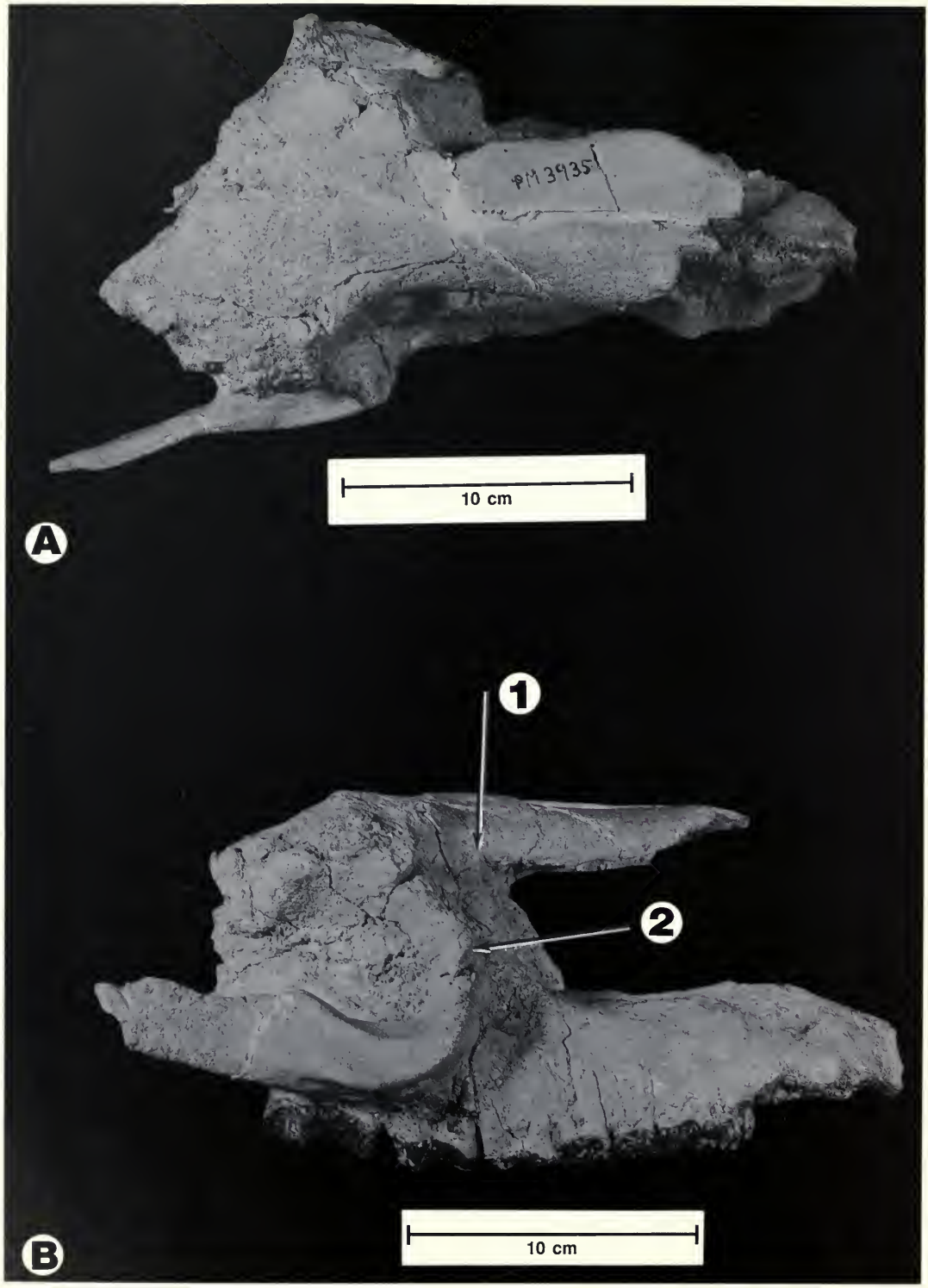

FIG. 7. *Metarhinus* sp., PM 3935, anterior half of skull. **A,** Dorsal view (FMNH neg. 85805). **B,** Lateral view (FMNH neg. 85806). Arrow 1 indicates posteriormost extension of the lateral nasal incision; arrow 2 indicates anteriormost extension of the orbit. Note that the lateral nasal incision does reach back to the orbit and the orbit is well defined by a raised bony rim, both characteristic of *Metarhinus*. (Figure continued on page 13.)

FIG. 7 (continued). C, PM 35932, lateral view (FMNH neg. 85982).

from the middle unit of the Adobe Town Member. *Metarhinus* is currently known from the Uintan elsewhere (Mader, 1989), including the Shoshonian (earliest Uintan) Subage (Flynn, 1986). PM 56023 is from near the base of the middle unit of the Adobe Town Member and, based on the distribution of other taxa, probably represents an earliest Uintan (Shoshonian Subage) occurrence of *Metarhinus* rather than an early Uintan occurrence. The same may be true of PM 3935, although it is from slightly higher in the section. The quarry sample (Appendix 2) is stratigraphically higher, in strata inferred to be early Uintan in age (based on other taxa).

***Dolichorhinus* sp. Hatcher, 1895**
(Fig. 8A,B)

REFERRED SPECIMENS—PM 3870, complete skull, from Loc. FM-2-57-WDT, $Twka_2$; PM 3873, complete skull, from Loc. FM-6-57-WDT, $Twka_2$.

DESCRIPTION—PM 3870 (Fig. 8A,B) is a complete skull missing only the right and left I^{1-2}. PM 3870 is a large titanothere with a P^2–M^3 length of 179.1 mm. PM 3870 possesses six upper incisors and large pointed canines. A small diastema is present between I^3 and the canine, and a larger diastema exists between the canine and P^1. P^1 has a single cusp, whereas P^{2-3} possess two labial and a single lingual cusp. M^{1-3} lack metaconules and protoconules, and M^3 possesses a small hypocone. The nasals broaden very slightly from their base and are slightly spoon-shaped. Two small horns are present dorsally and slightly anterior of the orbit. A large suborbital protuberance is present, subdivided into a smaller anterior flange and a larger posterior flange. The distinction between the two flanges, and their difference in size, are not as great in PM 3870 as we observed in other specimens of *Dolichorhinus* from the Uinta Formation (P 12175, P 12182). A broad shelf, rather than a sharp sagittal crest, defines the top of the cranium. PM 3870 is only slightly crushed, the most extensive crushing being on the posterior dorsal portion of the skull.

A second complete skull (PM 3873) is almost identical to PM 3870. PM 3873 shows a greater distinction, as well as a greater difference in size, between the anterior and posterior suborbital protuberances. PM 3873 is much less crushed than PM 3870 and the rounded nature of the cranial vertex is more obvious. There are two "pits" posterolingual to the horns above the orbit; these are not discernible on PM 3870.

DISCUSSION—*Dolichorhinus* has the most derived features of any Eocene titanothere discussed by Mader (1989). PM 3873 and PM 3870 may be confidently assigned to *Dolichorhinus* based on the presence in both specimens of all the unique derived characters that Mader (1989) assigned as diagnostic of the genus. These derived features are "hyperdolichocephalic skull; large suborbital protuberance with a small anterior flange and a larger posterior flange; small angular horn at frontonasal

FIG. 8. *Dolichorhinus* sp., PM 3870, complete skull. **A,** Dorsal view (FMNH neg. 85810). Arrow indicates low, broad sagittal crest typical of *Dolichorhinus*. Compare this to the sharply defined sagittal crest of *Mesatirhinus* in Figure 5A. **B,** Lateral view (FMNH neg. 85809).

boundary over orbit; rounded cranial vertex with no sagittal crest" (Mader, 1989, p. 468).

Both PM 3873 and PM 3870 are from high within the middle unit of the Adobe Town Member. *Dolichorhinus* is currently known from the Uintan elsewhere (Mader, 1989). Its occurrence here indicates an undifferentiated Uintan age assignment for the middle unit of the Adobe Town Member.

Brontotherioidea indeterminate

REFERRED SPECIMEN—PM 1676, partial skull and associated bone fragments, from Loc. FM-6-56-WDT, $Twka_2$.

DESCRIPTION—PM 1676 is approximately the same size as PM 36045 (*Mesatirhinus*), but is missing the orbital and nasal regions; the suborbital protuberance is as well developed as in PM 36045, although there is a more obvious division into smaller anterior and larger posterior flanges, similar to those in some specimens of *Dolichorhinus*. Preserved portions of the maxillary indicate that the lateral nasal incision was deep, possibly reaching back to the orbits.

DISCUSSION—PM 1676 cannot be confidently assigned to a taxon because the uniquely diagnostic parts of the nasal and orbital regions are not preserved. PM 1676 could be assigned to *Mesatirhinus* or *Rhadinorhinus* based on its size and the prominent suborbital protuberance. The specimen, however, is from the middle unit of the Adobe Town Member, which is thought to be earliest to early Uintan in age. If PM 1676 is *Mesatirhinus*, it would be the first Uintan occurrence of the taxon (see Mader, 1989). Alternatively, PM 1676 could be assigned to *Rhadinorhinus*, which is known from the Uintan of the Uinta Formation. The specimen also possesses a deep nasal incision, also a character of *Rhadinorhinus* (Mader, 1989). If PM 1676 is *Rhadinorhinus*, it would represent the first report of the genus from outside of the Uinta Formation of the Uinta Basin.

Infraorder Moropomorpha Schoch, 1984
Family Isectolophidae Peterson, 1919

Isectolophus latidens
(Osborn, Scott, & Speir, 1878)
(Fig. 9A)

REFERRED SPECIMEN—PM 55952, associated RM^{1-3}, LM^{2-3}, partial R&LM_3, from Loc. JJF 8-13-93-1, $Twka_1$.

DESCRIPTION—M^1 of PM 55952 (Fig. 9A) is narrower posteriorly than anteriorly, the paracone is the most prominent cusp, and the parastyle is rounded and well developed. M^2 is also narrower posteriorly and the parastyle is larger and more prominent than in M^1. In M^3 the metaloph is extended lingually compared to that of M^1 and M^2, giving M^3 a more trapezoidal outline. The parastyle is flattened and less prominent than on M^{1-2}. Prominent anterior, posterior, and lingual cingula are present on all upper molars.

Both M_3's are incomplete, lacking the anterior portion of the tooth. The hypolophid is well developed, with the cristid obliqua intersecting the protocristid slightly lingual to the protoconid. A large, well-developed hypoconulid is present, with a large notch in the posterolabial corner.

DISCUSSION—*Isectolophus* differs from *Homogalax* in the lack of protoconules and metaconules on M^{1-3} (rarely present in *Homogalax*), the lack of a metastylid on M_{1-3}, and in being larger in size (Radinsky, 1963). At present, two species of *Isectolophus* are recognized, *I. latidens* and *I. annectens*. They are differentiated by the larger size and the consistent presence of two lingual cusps on P^3 in *I. annectens*. Without the preservation of P^3 we can use only size to distinguish between *I. latidens* and *I. annectens*. On the basis of size (see Tables 2 and 3) we assign PM 55952 to *I. latidens*, as all measurements fall within the range reported for that species and outside the range of *I. annectens* (Radinsky, 1963).

PM 55952 is from the lower unit of the Adobe Town Member. The occurrence of *I. latidens* (PM 55952), a late Bridgerian taxon elsewhere, from the lower unit of the Adobe Town Member indicates a late Bridgerian age assignment for this unit.

Superfamily Chalicotherioidea Gill, 1872
Family Chalicotheriidae Gill, 1872

***Eomoropus amarorum* (Cope, 1881)**
(Fig. 9B–H)

REFERRED SPECIMENS—PM 1670, left dentary fragment with P_4–M_3, from Loc. FM-3-56-WDT, $Twka_2$; PM 2082, associated postcrania, including proximal end of femur, distal ends of tibia and fibula, astragalus, calcaneum, navicular, cuboid, lateral cuneiform, internal cuneiform, three com-

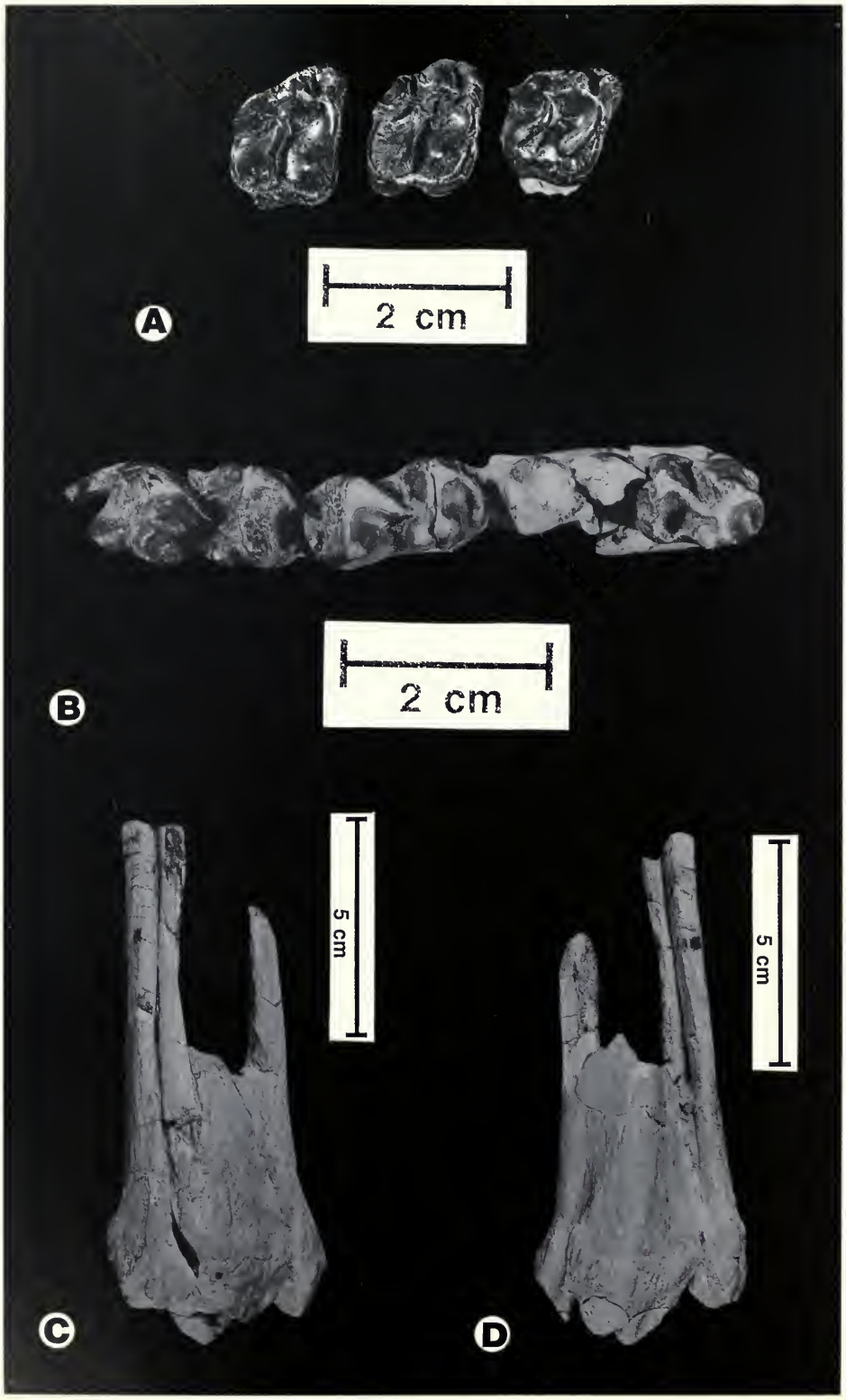

FIG. 9. See legend on opposite page.

FIG. 9. **A,** *Isectolophus latidens,* PM 55925, right M^{1-3} found in association, in occlusal view (FMNH neg. 85808). **B-H,** *Eomoropus amarorum.* **B,** PM 1670, left dentary fragment with P_4–M_3, in occlusal view (FMNH neg. 85814). **C-D,** PM 2082, anterior (FMNH neg. 85978) and posterior (FMNH neg. 85977) views of right tibia and fibula; note the well-developed fibula compared to the figured type specimen (see Osborne, 1913, Fig. 7). **E-G,** PM 2082, internal (FMNH neg. 85981), anterior (FMNH neg. 85980), and external (FMNH neg. 85979) views of right tarsus. **H,** PM 2082, three sesamoids (FMNH neg. 85976).

plete metatarsals (II, III, IV), two podials, and three sesamoids, from Loc. FM-1-56-WDT, $Twka_2$.

DESCRIPTION—The P_4 of PM 1670 (Fig. 9B) has a prominent metaconid and a small but distinct metastylid; the entoconid is very small. M_1 is worn and heavily damaged, but a well-developed entoconid is indicated by an upturn in the partial crown surface near the posterior lingual corner of the tooth. M_{2-3} are almost complete, with well-developed metastylids and very prominent entoconids compared to M_1. Small cingula are present along the anterior edge of M_{2-3}. M_{1-2} possess small hypoconulids; the posterior end of M_3 is broken, but the presence of a well-developed hypoconulid is indicated by the surface features that are preserved.

PM 2082 (Fig. 9C–H) comprises an almost complete distal right hind limb. There is a proximal

half of a badly crushed femur. Its head is attached by a short neck and has a well-developed foveal pit. Most of the greater trochanter is present; its anterior portion reaches a height equal to that of the head, while the posterior, broken portion exceeds the height of the head. As in the type (AMNH 5096, using Osborn's 1913 figures and descriptions), there is a marked fossa on the posterior surface. Second and third trochanters are similarly developed as in the type, although the latter is incomplete and may have extended a bit farther down the shaft than it does on the type (AMNH 5096). Length of the preserved proximal half is 260.0 mm, the distance from the head to the tip of the third trochanter is 150.0–160.0 mm, and the distance from the head to the middle of the second trochanter is 100.0–110.0 mm.

The tibia and fibula of PM 2082 (Fig. 9C,D) also correspond well with the type, except for one significant difference: the fibula of PM 2082 has a robust shaft and the type does not. Osborn (1913, p. 271) stated that "A distinctive feature is the marked reduction of the fibula; the lower portion of the shaft is so slender as to indicate that the central portion may have been incomplete. In *Moropus* the fibula has a complete shaft." We suspect that Osborn may have misinterpreted a weathered or incomplete shaft, in which case PM 2082 may give a better idea of the condition of the fibula of *Eomoropus* than does the type.

The tarsus of PM 2082 is almost complete (Fig. 9E–G). The three metatarsals, astragalus, and calcaneum have the same features and proportions as in the type. The same is true for the navicular, except that the facet for articulation with the calcaneum indicates a weaker articulation than Osborn noted for the type. Furthermore, in PM 2082 the cuboid articulates with the dorsal internal surface of the astragalus, and it is only on the surface that the two could be even slightly separated by the navicular. The posterior extension of the cuboid is a somewhat more massive and pronounced process than Osborn figured (1913, Fig. 4—B^2). The ectocuneiform (= external, or tarsal III) is broader than deep, and not as quadrate on its anterior face as is that of the type. The mesocuneiform (= middle, or tarsal II) is small and abbreviated, as Osborn described it in the type. Osborn (1913, Fig. 4—B^3) showed a bone he took to be the entocuneiform (= internal, or tarsal I), but that to us resembles a sesamoid. PM 2082 has three sesamoid bones (Fig. 9H), but unfortunately they were prepared free without their positions relative to the rest of the foot being noted. PM 2082 has no obvious facets which would indicate the presence of an entocuneiform.

The three metatarsals (II, III, IV) are complete bones. On the distal end each shows exactly the same sort of division into a keeled sesamoidal posterior face and a smoothly convex anterior phalangeal face, which Osborn describes for the metacarpals of the type. The best preserved of the two podial bones may belong to the fourth toe, as it makes a fair articulation with metatarsal IV.

DISCUSSION—The most recent revision of Eocene chalicotheres is that of Lucas and Schoch (1989). They recognized *Eomoropus amarorum* and *Grangeria anarisus* from the western United States, and *E. quadridentatus* and *G. canina* from the People's Republic of China. Radinsky (1964) recognized the same taxa, as well as a third Chinese species, *G.? major,* which Lucas and Schoch (1989) synonymized with *G. canina.*

Both Radinsky (1964) and Lucas and Schoch (1989) referred PM 1670 to *E. amarorum,* but did not discuss the specimen in detail. Its size (see Table 2) indicates that it should be assigned to a species of the smaller genus *Eomoropus* rather than of the larger genus *Grangeria.* According to Lucas and Schoch (1989), *E. amarorum* differs from *E. quadridentatus* in the more molariform premolars of *E. quadridentatus,* and in differences between P^{2-4} and P_2 of the two species. P_2 is not preserved in PM 1670, so direct comparisons cannot be made. P_4 is preserved, but we have found no comparative discussions of P_4 morphology between *E. amarorum* and *E. quadridentatus.* We have not been able to examine specimens of *E. quadridentatus* for comparison. Barring evidence to the contrary, we follow Radinsky (1964) and Lucas and Schoch (1989) and assign PM 1670 to *E. amarorum.* PM 2082 agrees well enough with Osborn's (1913) description of the type that we also assign it to *E. amarorum.*

Both PM 1670 and PM 2082 are from the middle unit of the Adobe Town Member. *Eomoropus amarorum* is currently known from the early Uintan elsewhere (Lucas and Schoch, 1989); its occurrence here indicates an early Uintan age assignment for some part of the middle unit of the Adobe Town Member.

Superfamily Tapiroidea Burnett, 1830
Family Helaletidae Osborn, 1892, in Osborn and Wortman, 1892

Helaletes nanus **(Marsh, 1871)**
(Fig. 10A)

REFERRED SPECIMEN—PM 55951 isolated right M_3, from Loc. FM-3-74-WDT, Twkk.

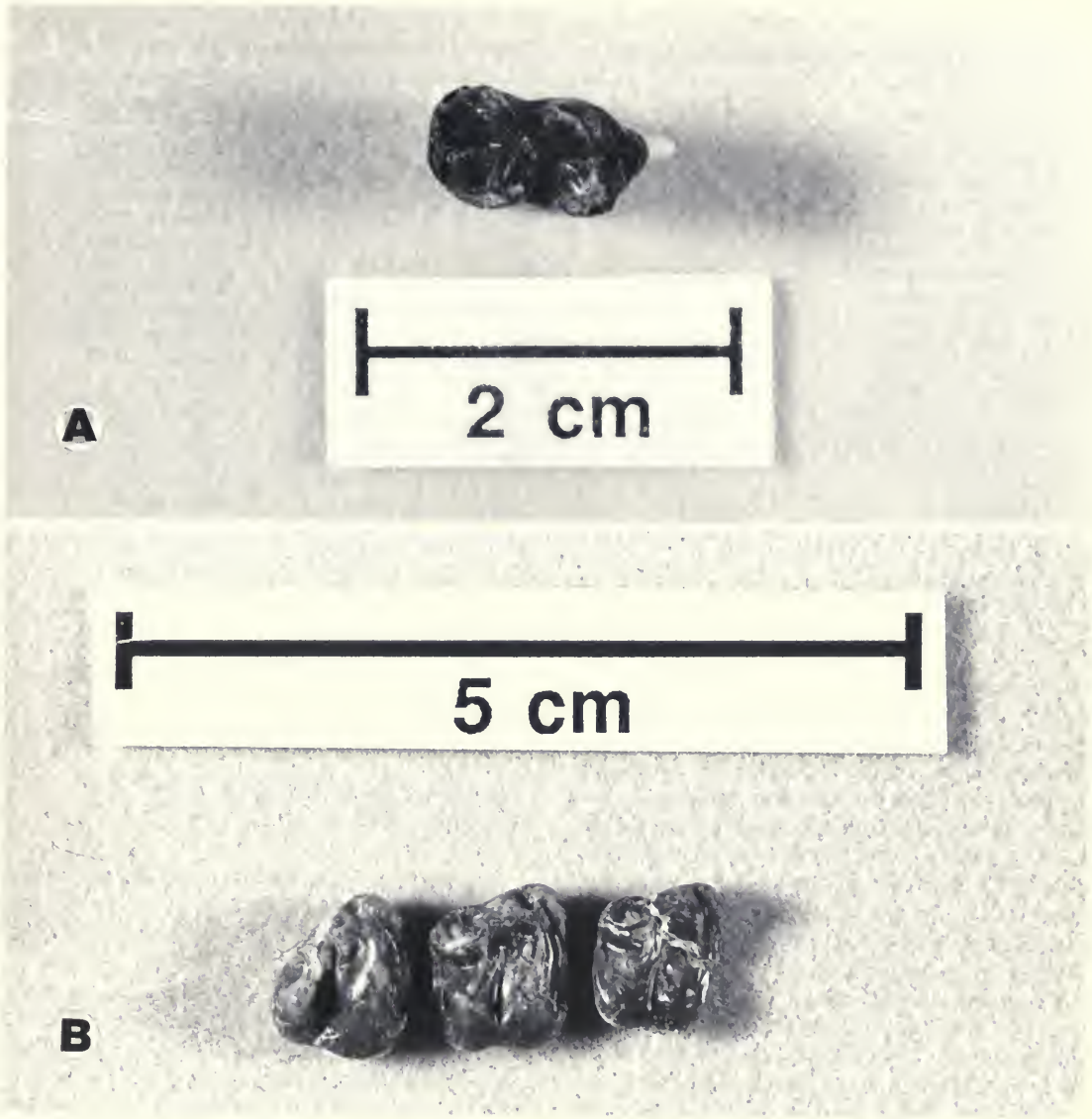

FIG. 10. **A**, *Helaletes nanus*, PM 55951, isolated right M_3, in occlusal view (FMNH neg. 85815). **B**, *Dilophodon minusculus*, PM 55709, right M^{1-3} found in association, in occlusal view (FMNH neg. 85825.7).

DESCRIPTION—PM 55951 (Fig. 10A) is almost complete, lacking only broken metaconid and entoconid tips. The roots lack only the proximal tips, and the posterior half of the tooth root shows a bony reinforcement under the hypoconulid characteristic of an M_3.

PM 55951 is distinctly bilophodont. The protoconid is very slightly anterior to the metaconid, whereas the hypoconid is distinctly more anterior than the entoconid. Both the paralophid and the protocristid are small, with the paralophid more pronounced and descending anteriorly from the protoconid, then turning sharply lingually. The protolophid is distinctly notched, while the hypolophid is only slightly notched. No lingual or labial cingula are present. A small anterior cingulum is present, starting lingually where the paralophid descends to the base of the metaconid, and running labially around the base of the protocone. A hypoconulid is present. It is medially situated, but closer to the entoconid than to the hypoconid. Small ridges connect the hypoconulid to the entoconid and the hypoconid. The ridge extending to the hypoconid is the longer of the two.

DISCUSSION—*Helaletes* is a small- to medium-

TABLE 1. Comparative dental measurements (in mm) of selected middle Eocene perissodactyl taxa.

Taxon	LM^{1-3}	LM_{1-3}	LP^2-M^3	Source
Isectolophus annectens	—	46.8	—	Radinsky, 1963
Isectolophus latidens	—	40.4	—	Radinsky, 1963
Helaletes nanus	31.6	—	—	Radinsky, 1963
Helaletes intermedius	44.4	—	—	Radinsky, 1963
Dilophodon minusculus	—	28.0	—	Radinsky, 1963
Dilophodon leonatus	—	25.1	—	Radinsky, 1963
Hyrachyus modestus	45–50	—	—	Radinsky, 1967b
Hyrachyus eximius	64	—	—	Radinsky, 1967b
Triplopus cubitalis	—	35	—	Radinsky, 1967a
Triplopus implicatus	—	46	—	Radinsky, 1967a
Amynodon advenus	93–131	90–117	—	Wall, 1982
Forstercooperia grandis	84–97	84–97	—	Lucas et al., 1981
Forstercooperia minuta	71–79	71–75	—	Lucas et al., 1981
Fouchia elyensis	19.2	18.6	—	Emry, 1989
Palaeosyops	—	—	129–165	Mader, 1989
Telmatherium	—	—	160–190	Mader, 1989
Mesatirhinus	—	—	128–145	Mader, 1989
Metarhinus	—	—	138–145	Mader, 1989
Rhadinorhinus	—	—	143–148	Mader, 1989
Dolichorhinus	—	—	164–193	Mader, 1989

sized helaletid. According to Radinsky (1963), *Helaletes* is characterized by the following combination of characters: canines small; P^1 simple; P^{2-4} submolariform with the metaloph less prominent than the protoloph and a tendency for the hypocone to separate off from the protocone; metacone of M^{1-2} slightly convex to flat and slightly shortened; M^3 metaloph relatively short; P_1 absent; trigonids of P_{2-4} low but with long paracristids; small entoconid present on P_{3-4}; M_3 retains a hypoconulid; greatly enlarged nasal incision.

At present, two species of *Helaletes* are recognized: *H. nanus* and *H. intermedius*. They are distinguished from each other most readily on the basis of size (see Table 1). In addition, the P^3 metaloph of *H. nanus* extends toward an incipient hypocone, in contrast to *H. intermedius*, where the metaloph extends toward the protocone, bypassing the hypocone (Radinsky, 1963).

PM 55951 is referred to *H. nanus* on the basis of size (see Table 2) and the presence of an M_3 hypoconulid. PM 55951 is small for *H. nanus* compared to measurements reported by Radinsky (1963), and is smaller than any measurements reported for *H. intermedius*. PM 55951 is closer in size to reported measurements (Radinsky, 1963) of *Dilophodon minusculus* than to either species of *Helaletes*; however, *D. minusculus* lacks an M_3 hypoconulid.

PM 55951 comes from the Kinney Rim Member, the lowest unit of the formation. *Helaletes nanus* is currently known from the Bridgerian elsewhere, and its occurrence here indicates an undifferentiated Bridgerian age assignment for the Kinney Rim Member.

Dilophodon minusculus Scott, 1883
(Fig. 10B)

REFERRED SPECIMENS—PM 55709, associated right M^{1-3}, from Loc. JJF 7-25-92-1, $Twka_2$; PM 55711, isolated left M^3, from Loc. FM-6-56-WDT, $Twka_2$.

DESCRIPTION—The M^1 of PM 55709 (Fig. 10B) has a posterolabially directed metastyle and a metacone that is very slightly convex labially. The parastyle is very distinct, with a notch between it and the paracone. Anterior and posterior cingula are present, as is a cingulum labial to the metacone. In PM 55709, the M^2 differs from the M^1 in having a broader notch between the parastyle and paracone (this may be due to differences in wear stage), a metacone that is very slightly concave labially, and a slightly larger parastyle. The M^3 of PM 55709 has a very small metacone that is also more lingually deflected than in M^{1-2}. In addition, the labial surface of the metacone is flat and has no associated cingulum. The posterior cingulum of M^3 is smaller than in M^1 or M^2.

PM 55711 is very similar to PM 55709 but has a more robust parastyle and metastyle. PM 55711 is longer than PM 55709 (Table 3).

DISCUSSION—*Dilophodon* is a very small helaletid. According to Radinsky (1963), *Dilophodon* is recognized by the following combination of

TABLE 2. Length–width measurements (in mm) of all lower cheektooth specimens reported here.

	P_2		P_3		P_4		M_1			M_2			M_3		
	L	W	L	W	L	W	L	AW	PW	L	AW	PW	L	AW	PW
Epihippus gracilis															
PM 55311	–	–	7.0	4.3	7.4	4.9	7.5	5.5	–	8.7	5.2	–	–	–	–
Orohippus sp.															
PM 39944	–	–	–	–	–	–	–	–	–	–	–	–	10.7	5.6	5.0
Isectolophus latidens															
PM 55952	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8.9
Eomoropus amarorum															
PM 1670	–	–	–	–	11.5	8.9	11.1	–	–	16.3	9.5	9.3	20.6	10.5	–
Helaletes nanus															
PM 55951	–	–	–	–	–	–	–	–	–	–	–	–	11.3	6.3	–
Hyrachyus modestus															
PM 55710	–	–	10.5	6.5	12.7	–	14.7	9.1	–	15.5	10.7	–	17.4	11.0	–
PM 55959	–	–	–	–	11.3	–	–	–	–	–	–	–	–	–	–
PM 55712	–	–	–	–	–	–	–	–	–	–	10.7	–	–	–	–
Triplopus cubitalis															
PM 55708	–	–	8.5	6.0	9.3	7.0	~11.3	8.2	–	12.9	9.1	–	14.5	5.0	–
PM 28365	–	–	8.3	5.5	8.9	6.7	11.1	7.4	–	12.6	~7.9	–	13.2	8.0	–
Triplopus implicatus															
PM 3228	–	–	–	–	–	–	–	–	–	16.7	10.3	–	–	–	–
Amynodon advenus															
PM 1514	–	–	–	–	–	–	–	–	–	–	25.8	–	39.4	24.0	–
PM 3874	11.6	9.1	–	12.5	21.4	16.4	27.8	~18.2	–	34.8	~21.3	–	~38.7	–	–
PM 51597	–	–	–	–	–	–	–	–	~20.7	~33.6	21.8	24.6	~40.2	~23.7	–

L indicated length; W, width; AW, anterior width; and PW, posterior width.

characters: premolar molarization retarded compared to the *Helaletes–Colodon* line; M^{1-2} metacone lingually displaced, slightly convex labially, and with a small labial cingulum; short lower postcanine diastema; P_1 absent; M_3 hypoconulid not present.

At present, two species of *Dilophodon* are recognized, *D. minusculus* (late Bridgerian) and *D. leotanus* (late Uintan). They are distinguished (Radinsky, 1963) from each other based on the following: size (see Table 1); P^2 with two labial cusps in *D. leotanus,* only one in *D. minusculus*; P^{3-4} relatively nonmolariform in *D. minusculus,* submolariform in *D. leotanus*; symphysis begins anterior to P_2 in *D. minusculus,* whereas it is posterior to P_2 in *D. leotanus*; P_{2-4} long and narrow in *D. minusculus* compared to short and narrow in *D. leotanus.*

Both specimens reported here compare well with *D. minusculus* measurements reported by Radinsky (1963). *D. leotanus,* a late Uintan form, is smaller than *D. minusculus,* but the size difference is not great (see Table 1). Even so, PM 55709 and PM 55711 are closer to *D. minusculus* than to *D. leotanus* (see Table 3). In addition, the concavity of M^{1-2} metacones of PM 55709 are closer to *D. minusculus,* as *D. leotanus* has more convex M^{1-2} metacones.

Radinsky (1963) recognized no early Uintan species of *Dilophodon* and did not preclude the evolution of the late Uintan *D. leotanus* directly from the late Bridgerian *D. minusculus.*

Black (1979) reported *D. leotanus* from the late Eocene Badwater Creek Fauna of central Wyoming. The sizes of the upper and lower molars of those specimens are closer to *D. minusculus,* whereas the anterior teeth are closer in size to *D. leotanus.* The possibility thus exists that *D. leotanus* molars overlap in size with those of *D. minusculus,* and if specimens are found without the anterior dentitions preserved, the two taxa may be confused.

Schiebout (1977) reports *Dilophodon* sp. indet. from the La Jolla and Poway groups of San Diego County, California. Schiebout considers these specimens intermediate between *D. minusculus* and *D. leotanus.* "Early Uintan" (now considered earliest Uintan [Flynn, 1986]) *D. minusculus* is reported from the Tepee Trail Formation of northwestern Wyoming by MacFadden (1980).

Both specimens reported here were collected low within the middle unit of the Adobe Town Member, both from approximately bed 630. *Dilophodon minusculus* is currently known from the late Bridgerian to earliest Uintan elsewhere, and *D. leotanus* is known from the late Uintan elsewhere (Radinsky, 1963). Assuming that *D. leotanus* is derived from *D. minusculus,* this leaves us with no species of *Dilophodon* from the early Uintan. Flynn (1986) lists *Dilophodon,* presumably *D. minusculus,* based on MacFadden (1980), as a characteristic earliest Uintan taxon but gives no species-level data or discussion. This is an important distinction here because both PM 55709 and PM 55711 are from low within the middle unit of the Adobe Town Member, previously thought to be early Uintan. The co-occurrence of *D. minusculus* with characteristic early Uintan taxa would indicate an earliest Uintan, rather than late Bridgerian or early Uintan, age for some lower portion of the middle unit of the Adobe Town Member.

Superfamily Rhinocerotoidea Gill, 1872

Hyrachyus modestus (Leidy, 1870)

(Fig. 11A,B)

REFERRED SPECIMENS—PM 37284, RM^2 in maxillary fragment, from Loc. FM-11-70-WDT, Twkk, bed 527; PM 55358, LP^{2-4} in maxillary fragment with possibly associated postcranial fragments, from Loc. JJF 7-24-90-1, $Twka_1$; PM 55710, RP_3–M_3 in dentary fragment, from Loc. JJF 7-24-90-1, $Twka_1$; PM 55712, RM_2 with associated dentary fragment, from Loc. FM-1-58-WDT, $Twka_1$; PM 55959, left dentary fragment with P_4 and partial M_2, from Loc. JJF 7-28-92-2, $Twka_1$.

DESCRIPTION—PM 55710 (Fig. 11A) preserves a portion of the symphysis showing a diastema between the canine and P_1. The symphysis extends beneath the anterior half of P_2. The posterior mental foramen is located beneath the anterior half of M_3. PM 55710 is the most complete *H. modestus* dentary in the FMNH collections, possessing the right P_3–M_3. The alveoli of the anterior premolars indicate that P_1 was single-rooted and P_2 was probably small, unmolarized, and double-rooted. P_3 has a well-developed protocristid and a small, sharply curved paracristid; the hypolophid and entoconid are small and poorly developed; the hypoconid is distinct but lower than the metaconid and protoconid. P_4 is larger and more molarized than P_3; the hypolophid and entoconid are more developed but still lower than the metaconid and protoconid.

TABLE 3. Length–width measurements (in mm) of all upper cheektooth specimens reported here.

	P^2		P^3		P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W	L	W
Orohippus sp.												
PM 55790	–	–	–	–	–	–	6.9	7.5	–	–	–	–
Isectolophus latidens												
PM 55952	–	–	–	–	–	–	12.0	14.9	13.2	15.8	13.0	15.4
Dilophodon minusculus												
PM 55709	–	–	–	–	–	–	7.3	~9.8	8.6	10.6	8.7	10.3
PM 55711	–	–	–	–	–	–	–	–	–	–	9.0	10.0
Hyrachyus modestus												
PM 37284	–	–	–	–	–	–	–	–	16.0	17.2	–	–
PM 55358	8.5	8.7	~9.8	11.9	~10.7	14.1	–	–	–	–	–	–
Hyrachyus eximius												
PM 26128	–	–	–	–	–	–	–	–	–	–	21.5	24.3
PM 55867	–	–	–	–	–	–	–	–	–	–	24.2	–
Triplopus implicatus												
CM 18464	–	–	10.1	~12.5	10.4	~13.4	13.1	14.9	16.0	~16.3	~15.4	~15.8
cf. *Forstercooperia minuta*												
PM 1682	–	–	–	–	–	–	–	–	–	–	24.5	~25.0
Hyracodontidae indet.												
PM 3937	–	–	–	–	–	–	~38.1	~39.5	–	–	–	–
Amynodon advenus												
PM 1088	–	14.0	18.7	21.0	19.1	26.4	33.2	31.5	–	35.3	–	–
CM 9382	–	–	~18.5	–	~20.5	–	~29.3	–	–	–	–	–

L indicates length; W, width.

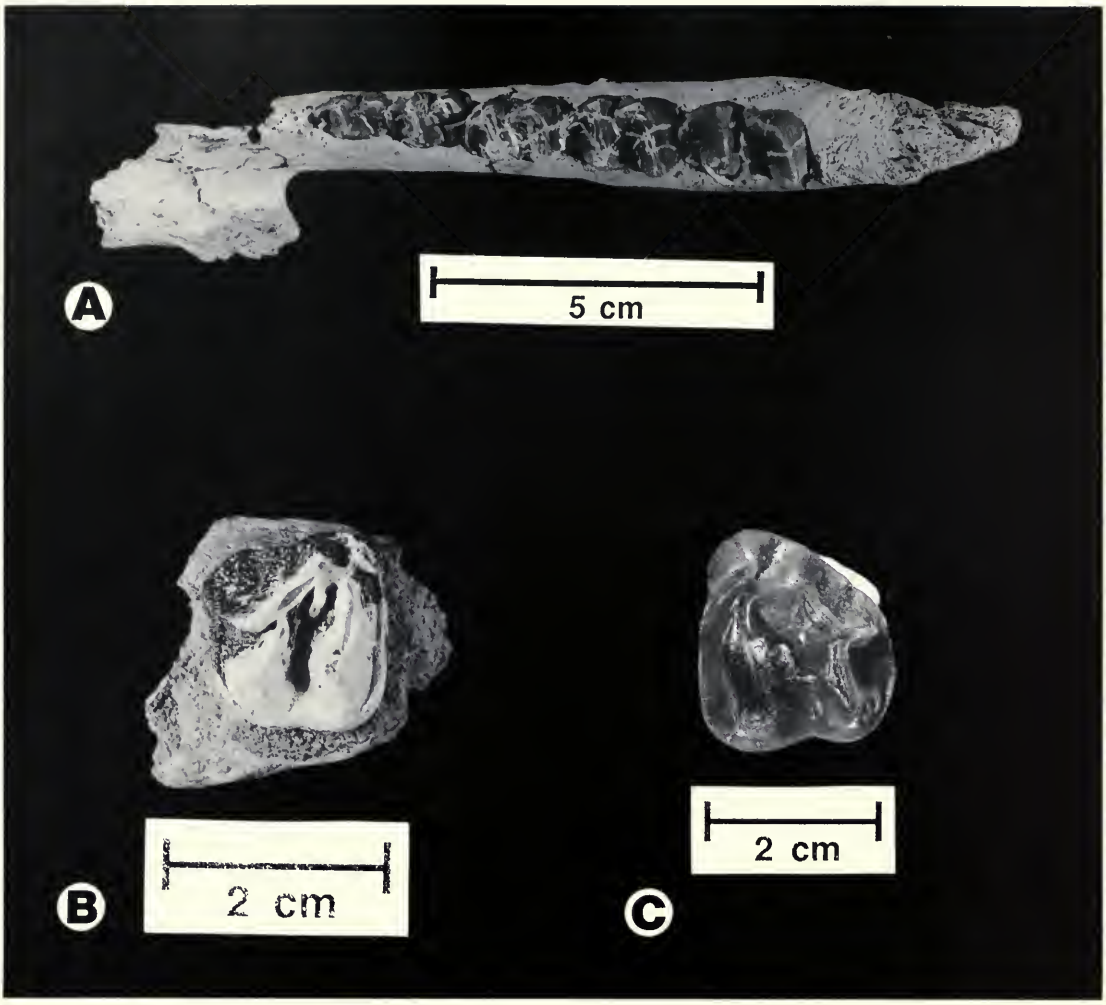

FIG. 11. **A,** *Hyrachyus modestus,* PM 55710, right dentary fragment with P_3–M_3, in occlusal view (FMNH neg. 85816). **B,** *Hyrachyus modestus,* PM 37284, right maxillary fragment with M^2, in occlusal view (FMNH neg. 85817). **C,** *Hyrachyus eximius,* PM 26128, isolated left M^3, in occlusal view (FMNH neg. 85777.11).

M_{1-3} are very similar, becoming progressively larger in size from M_1 to M_3. The molar protocristids and hypolophids are almost equal in size, compared to those of the premolars, in which the protocristids and hypolophids differ in size. The hypolophid on M_3 runs slightly more diagonally across the tooth rather than more transversely as in M_{1-2}. M_3 lacks a hypoconulid.

PM 55358 is a left maxillary fragment preserving P^2 and the lingual half of P^{3-4}. All three premolars are nonmolariform with no indication of a second lingual cusp. P^2 has two indistinct labial cusps.

PM 37284 (Fig. 11B) is a right maxillary fragment preserving a complete M^2. It possesses a slightly concave labial metacone, with a small labial cingulum. The metacone is deflected lingually to the midline of the tooth. The paracone is the most prominent cusp of the tooth. The parastyle is large and distinct from the paracone. The protoloph is long and possesses a small paraconule, which is slightly labial to the midline of the tooth. The metaloph is much shorter than the protoloph and possesses a very small metaconule positioned along the midline of the tooth. A distinct ridge runs from the paracone toward the center of the tooth.

DISCUSSION—A combination of characters is used to recognize *Hyrachyus.* These include: re-

tention of P_1; nonmolariform to submolariform premolars; no M_3 hypoconulid; and size (Radinsky, 1967b). At present, two species of North American *Hyrachyus* are recognized, *H. modestus* and *H. eximius*. Both species are reported here from the Washakie Formation. They are distinguished from each other on the basis of size (see Table 1) (Radinsky, 1967b). Schoch (1989, p. 310) considered Radinsky's revision of *Hyrachyus* to one genus and two species to be too "lumped," but gave no species-level revisions. Until further taxonomic revision, we follow Radinsky (1967b).

PM 55710, a right dentary with P_3–M_3 and alveoli of P_{1-2}, cannot be assigned to *Helaletes nanus*, as its M_3 lacks a hypoconulid. Length–width measurements of the specimens reported here (see Tables 2 and 3) compare well with those given by Radinsky (1967b) for *H. modestus* from the Bridger Formation. Radinsky (1967b) doubted all previous reports of *Hyrachyus* from the Washakie Formation, giving either incorrect locality data or misidentification of *Triplopus* specimens as the reason(s). He stated that *Triplopus* specimens are easily confused with *Hyrachyus*, especially when M^3 is not preserved.

This presents a problem, however, as no specimens of *H. modestus* reported here preserve M^3. *Hyrachyus modestus* is the smallest species of *Hyrachyus*, and it overlaps in size with *Triplopus implicatus*, also known from the Washakie Formation. A second species of *Triplopus* from the Washakie Formation, *T. cubitalis*, is much smaller than *H. modestus* (see Table 1) (Radinsky, 1967a). PM 55710 has an M_{1-3} length of 47.2 mm, only slightly larger than *T. implicatus* reported by Radinsky (1967a) (see Table 1). Unfortunately, no discrete morphological characters are known to distinguish *Hyrachyus* and *Triplopus* lower dentitions. This makes the identification of lower dentitions of these two taxa tentative, leaving both *H. modestus* and *T. implicatus* from the Washakie Formation of little biostratigraphic utility. We tentatively assign these specimens to *Hyrachyus modestus* rather than *Triplopus implicatus* because of the late Bridgerian age of the Washakie Formation strata in which they occur, including the Kinney Rim Member (PM 37284) and from the lower unit of the Adobe Town Member (PM 55701, 55358, 55712). *Hyrachyus modestus* has a late Bridgerian last occurrence elsewhere (Krishtalka et al., 1987, and references therein), whereas *Triplopus implicatus* has an early Uintan first occurrence elsewhere (Table 4).

***Hyrachyus eximius* Leidy, 1871**
(Fig. 11C)

REFERRED SPECIMENS—PM 26128, isolated left M^3, from Loc. FM-11-70-WDT, Twkk, bed 527; PM 55867, weathered fragments of what was probably a complete skeleton, including partial left and right M^3, from Loc. JJF 7-28-92-1, $Twka_1$.

DESCRIPTION—PM 26128 (Fig. 11C) has a distinct protoloph and metaloph. The protocone and hypocone are only slightly deflected posteriorly with reference to the paracone and metacone. A well-developed metastyle runs perpendicular to the metaloph. The paracone is large and distinct from the rest of the ectoloph. The parastyle is large, with a deep notch separating it from the paracone. The tooth is moderately worn, with a distinct groove separating the paracone and the protocone on the occlusal surface. No labial or lingual cingula are present. Small anterior and posterior cingula are present.

PM 55867 is very similar to PM 26128. The metastyle is slightly larger and the anterior and posterior cingula are slightly larger. In addition, a small cingulum is present lingually between the protocone and hypocone. All these differences may be attributed to differences in wear stages between the two specimens, with PM 55867 being much less worn than PM 26128. The parastyle and paracone are broken on PM 55867, thereby limiting comparison with PM 26128.

DISCUSSION—PM 26128 is a left M^3 and is confidently assigned to *H. eximius*, firmly establishing the presence of the genus *Hyrachyus* in the Washakie Formation, contrary to the conclusions of Radinsky (1967b). This specimen (see Table 3) falls within the observed size range reported for the species by Radinsky (1967b). In addition, possession of a metacone perpendicular to the metaloph and a large robust parastyle with a deep groove separating it from the paracone distinguish it from *Triplopus*.

PM 26128 is from bed 527, near the base of the Kinney Rim Member. At present, the temporal range of *H. eximius* elsewhere consists of a late Bridgerian first occurrence and an earliest Uintan last occurrence. The presence of *H. eximius* near the base of the Kinney Rim Member indicates that the lower part of the Washakie Formation is late Bridgerian or younger, and the early–late Bridgerian boundary is below bed 527 and probably lies within the underlying Green River Formation (see biostratigraphic section for further discussion).

Family Hyracodontidae Cope, 1879

Triplopus cubitalis (Cope, 1880)
(Fig. 12A)

REFERRED SPECIMENS—PM 28365, right dentary fragment with P_3–M_3, from Loc. FM-12-70-WDT, $Twka_2$; PM 55708, a fragmentary left dentary with P_3–M_3, from Loc. JJF 7-25-92-2, $Twka_2$, bed 630.

DESCRIPTION—PM 28365 (Fig. 12A) is moderately bilophodont, with well-developed paralophids and metalophids. Both the P_3 and P_4 have small hypolophids, making the metalophids the most prominent feature of the posterior half of these teeth. On P_4, however, there is a small posterolingual swelling, indicating an incipient entoconid. This swelling is separated from the small hypolophid by a small groove. Such a swelling could be considered a small cingulum rather than an incipient entoconid; it should be noted, however, that no cingula are present in this position on any other tooth except for a very small posterolingual cingulum on M_3. Small anterolingual cingula are present on P_3 and P_4. For all the teeth the protolophid is higher than the hypolophid; this is true even for M_1, the most heavily worn tooth. In addition to the complete teeth, the alveoli are preserved for P_1 and P_2. P_2 is double-rooted and the posterior mental foramen lies directly beneath it. The P_1 alveolus is incomplete on its anterior border, and it may be single- or double-rooted. Radinsky (1967a, Fig. 1) shows P_1 to be single-rooted in *T. cubitalis*.

PM 55708 is very similar to PM 28365, differing only in being slightly larger (see Table 2).

DISCUSSION—*Triplopus* is a small hyracondontid recognized (Radinsky, 1967a) by the following combination of characters: dentition unreduced; incisors equal in size and spatulate; premolars nonmolariform to submolariform; M^3 with small metacone; and a tridactyl manus.

Two species of *Triplopus* are currently recognized from the Washakie Formation, *T. cubitalis* and *T. implicatus* (Radinsky, 1967a). They are distinguished from each other on the basis of size (see Table 1) and are assigned to *Triplopus* rather than *Hyrachyus* because of their Uintan age in the Washakie Formation and known ranges elsewhere. PM 55708 is assigned to *T. cubitalis* rather than *T. implicatus* because of its smaller size (see Table 2).

PM 55708 is from ~bed 630, near the base of the middle unit of the Adobe Town Member. Radinsky (1967a) stated that "All specimens of *Triplopus cubitalis* come from the Washakie Formation of the Washakie Basin, Wyoming, ..." Thus, their presence in FMNH collections is not surprising, and adds nothing to their biochronologic utility. Furthermore, we have been unable to locate subsequent reports of *T. cubitalis* from elsewhere in the western interior.

Triplopus implicatus (Cope, 1873)
(Fig. 12B)

REFERRED SPECIMENS—PM 3228, isolated right M_3, from Loc. FM-8-57-WDT, $Twka_2$; CM 18464, partial skull with LP^4–M^3 and RP^3–M^3 and associated dentaries, from Loc. "west rim of Adobe Town about 4 miles south of Haystack Mt."

DESCRIPTION—PM 3228 is only moderately bilophodont, with a well-developed paralophid and metalophid. The paralophid is the larger of the two lophids, and runs anteriorly from the protoconid and then lingually along the anterior margin of the tooth. The smaller metalophid runs anteriorly from the hypoconid to the posterior base of the protoconid. The protolophid is slightly higher than the hypolophid. A small cingulum is present on the posterolingual corner of the tooth. In addition, a very small, faint cingular ridge runs along almost the entire base of the tooth, being absent only on the anterior margin.

In some features PM 3228 could be mistaken for an M_2. The angle between the posterior and anterior halves of the root is not as great as that seen in the M_3 of other specimens of *Triplopus* (PM 55708, for example), but is closer to that seen in the M_2. Even so, the angle is still fairly high and the thickness of the posterior half of the root is more similar to that of an M_3 than to either an M_2 or M_1.

The M^3 of CM 18464 (Fig. 12B) has a very small metastyle and M^{1-3} have small, reduced (compared to *Hyrachyus*) parastyles. Both P^{3-4} are submolariform.

DISCUSSION—Measurements of PM 3228 (see Table 2) are well within the range of those reported for the larger *T. implicatus* and outside of those reported for the smaller *T. cubitalis* (Radinsky, 1967a).

PM 3228 is from the middle unit of the Adobe Town Member. As with *T. cubitalis, T. implicatus* is known only from the Washakie Formation and is thus of limited biochronologic utility. We suspect, as did Radinsky (1967a, p. 14), that larger sample sizes will result in the synonymy of *Tri-*

FIG. 12. **A,** *Triplopus cubitalis,* PM 28365, right dentary fragment with P_3–M_3, in occlusal view (FMNH neg. 85777.19). **B,** *Triplopus implicatus,* CM 18464, right maxillary fragment with P^3–M^3, in occlusal view (FMNH neg. 85824.26).

plopus species from the Uinta and Washakie formations.

CM 18464 was listed by Radinsky (1967a, p. 13) as a specimen of *T. implicatus*. He did not, however, list it as a specimen preserving the upper molars (see Radinsky, 1967a, p. 12). CM 18464 does preserve the upper right and left molars. In overall morphology, CM 18464 is assignable to *Triplopus* and its size (see Table 3) is within the range reported for *T. implicatus*.

cf. *Forstercooperia minuta*
Lucas, Schoch, & Manning, 1981

REFERRED SPECIMEN—PM 1682, an isolated left M^3, from Loc. FM-5-56-WDT, $Twka_2$.

DESCRIPTION—PM 1682 is not complete, as it lacks a parastyle, the labial base of the paracone, and the anterior portion of the hypocone. The ectoloph and metaloph are not readily distinguished, giving the tooth a generally triangular shape. The metacone intercepts the metaloph lingually just past the midline of the tooth; the metastyle is almost perpendicular to the metaloph. The protoloph is slightly crescent-shaped.

DISCUSSION—*Forstercooperia* is a medium- to large-sized hyracodontid recognized (Radinsky, 1967a) by the following combination of characters: size (see Table 1); dentition unreduced compared to that of *Hyrachyus*; incisors approximately equal in size and pointed; canines medium-sized and stubby; premolars nonmolariform to submolariform; M^3 metacone small to absent. Wood (1938) first coined the name *Forstercooperia* for the preoccupied genus *Cooperia*. Radinsky (1967a) recognized five species of *Forstercooperia*, four from Asia and one, *F.? grandis* (= *Hyrachyus grandis* Wood, 1934), from the Uinta and Washakie formations. Most recently, Lucas et al. (1981) recognized only three species of *Forstercooperia*: *F. totadentata* (middle to late Eocene of Asia), *F. grandis* (middle to late Eocene of Asia, late Eocene of North America), and *F. minuta* (middle to late Eocene of Asia, late Eocene of North America).

PM 1682 is almost identical morphologically to the M^3 of UCMP 69722, a complete skull of *F. grandis* figured by Radinsky (1967a, Fig. 11). Its size, however (see Table 3), is closer to measurements reported for the smaller *F. minuta* and well outside the range of reported measurements for the larger *F. grandis* (Lucas et al., 1981). The paucity of specimens and the fragmentary nature of PM 1682 preclude a more confident identification. If accurate, this is the first report of *F. minuta* from the Washakie Formation.

PM 1682 is from the middle unit of the Adobe Town Member. North American *F. minuta* is currently known from the Galisteo Formation of north-central New Mexico, which is of Duchesnean age (Lucas et al., 1981; Lucas & Sobus, 1989), and the Tepee Trail Formation of northwestern Wyoming, which is of Bridgerian to early Uintan age (Eaton, 1985). These age occurrences are consistent with an earliest–early Uintan age assignment for the middle unit of the Adobe Town Member, as indicated by other taxa.

Hyracodontidae indeterminate

REFERRED SPECIMEN—PM 3937, right maxillary fragment with fragmentary P^4–M^2, associated atlas, from Loc. FM-8-57-WDT, $Twka_2$.

DESCRIPTION—PM 3937 possesses three highly fractured teeth that are interpreted here as P^4–M^2. P^4 appears to have a large, well-separated protocone and hypocone, but lacks a well-developed metastyle. M^1 possesses a high paracone and only a small vestige of a parastyle. The metastyle is missing, but remnants of enamel present on the ectoloph and metaloph indicate that a posterolabially deflected metastyle was present. M^2 is very poorly preserved and adds no further information.

DISCUSSION—PM 3937 is assigned to the Hyracodontidae based on overall molar morphology and size. Although it is broken and fragmentary, this specimen appears to have been larger (see Table 3) than *Forstercooperia grandis* and is close to measurements reported for *F. totadentata* from China (Lucas et al., 1981). Because of the fragmentary nature of the specimen, we do not attempt a more specific identification.

Family Amynodontidae Scott and Osborn, 1883

***Amynodon advenus* Marsh, 1877**
(Fig. 13)

REFERRED SPECIMENS—PM 1088, paired right and left maxillary dentitions with RP^2–M^2 and LP^2–M^2, from Loc. given only as "Top of Haystack Mt."; PM 3874, dentary with LC–M_2 and RP_3–M_2, from FM-8-57-WDT, $Twka_2$; PM 1514, right dentary fragment with M_3 and partial M_2, associated calcaneum and postcranial fragments, from Loc. FM-

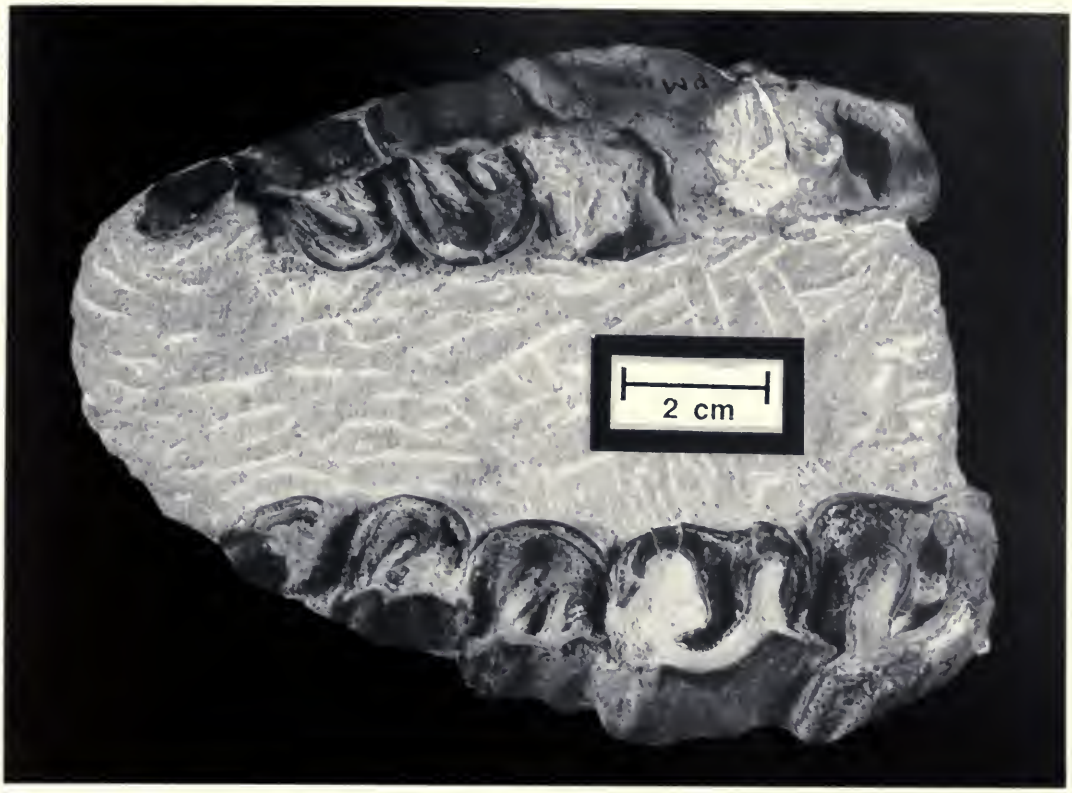

FIG. 13. *Amynodon advenus,* PM 1088, right and left maxillary dentitions (in matrix) showing RP^2–M^2 and LP^2–M^2, in occlusal view (FMNH neg. 85777.5).

10-56-WDT, $Twka_2$; CM 9382, associated LP^3–M^2 and tooth fragments, from Loc. given only as "Haystack Mt."; PM 51597, left dentary fragment with partial M_{1-3}, and associated incisors, from Loc. FM-6-73-WDT, $Twka_2$.

DESCRIPTION—In PM 1088 (Fig. 13) both second premolars and both second molars are damaged; the third molars are both missing. The fourth premolars are large and submolariform, and the third and fourth premolars have a continuous, heavy lingual cingulum. In PM 3874, the left and right P_2 alveoli show them to be double-rooted, and the P_1 is absent. In addition, a distinct labial groove separates the trigonids and talonids on P_4–M_2. This is also true for PM 1514. However, PM 1514 is more worn than PM 3874, making the lingual groove separating the trigonid and talonid less obvious. CM 9382 is indistinguishable from PM 1088.

DISCUSSION—*Amynodon* is recognized (Wall, 1982) by the following combination of characters: large double-rooted P_2; a distinct labial groove separating trigonid and talonid on molars; length of upper and lower premolar series is approximately half that of molar series (see Table 1); P^4 large and submolariform; and M^3 metastyle less labially deflected than in more derived amynodonts. At present, only two North American species of *Amynodon* are recognized, *A. advenus* and the much smaller *A. reedi* (Wilson & Schiebout, 1981; Wall, 1982).

The loss of P_1, a large double-rooted P_2, and size (see Table 2) allow the lower dentitions to be confidently assigned to *A. advenus.* Unfortunately, PM 1088 lacks the diagnostic metastyle condition on M^3; even so, it possesses a large submolariform P^4 and is of appropriate size (see Table 3) for assignment to *A. advenus.*

All *Amynodon* specimens reported here are from the middle unit of the Adobe Town Member. *Amynodon* is currently known from the earliest Uintan (Shoshonian Subage) through the Duchesnean elsewhere (Krishtalka et al., 1987), although we are unsure if *Amynodon* has a Duchesnean last occurrence. *Amynodon* is currently used as the de-

fining taxon for the base of the Uintan NALMA (Flynn, 1986). The lowest stratigraphic occurrence of *Amynodon* within the Washakie Formation is PM 3874 from the northwest flank of Haystack Mountain. This is stratigraphically higher than Granger's (1909) bed 11, which was his Bridgerian–Uintan boundary. We discuss the position of the Bridgerian–Uintan boundary in the biostratigraphic section of this paper.

Biostratigraphy

Overview

Granger (1909) was the first to divide the Washakie Formation (see Fig. 3). Granger called the lower half of the formation "Washakie A" (~260 ft/79 m, beds 1–10) and considered it to correspond faunally to the "Bridger C–D" based on the presence of *Uintatherium, Manteoceras, Mesatirhinus, Notharctus, Hyrachyus,* and *Sinopa.* He called the upper half of the formation "Washakie B" (~380 ft/116 m, beds 12–22) and considered it to correspond faunally to the "Uinta A–B" based on the presence of *Eobasileus, Achaenodon, Amynodon, Dolichorhinus,* and *Metarhinus.* Granger considered the base of the Washakie Formation to be the "lower brown sandstone," a sequence of sandstones, varying in thickness, that weather to a reddish brown and form a distinct rim around much of the basin. Granger considered the summit of Haystack Mountain to be the top of the Washakie Formation. Haystack Mountain (as discussed by Turnbull, 1978) is a high topographic feature in the north–northeast portion of the basin, which Granger assumed included the stratigraphically highest beds in the formation.

Roehler (1973) formally divided the Washakie Formation into two members, the lower Kinney Rim Member (~900 ft/270 m, beds 515–568) and the upper Adobe Town Member (≈2,300 ft/700 m, beds 569–708). He also informally divided the Adobe Town Member into lower, middle, and upper units (see Fig. 2). As noted earlier, the Washakie Formation as defined by Roehler (1973) is more inclusive than Granger's (1909) concept of the Washakie Formation. Roehler's (1973) Kinney Rim Member and the upper unit of the Adobe Town Member were not recognized by Granger (1909). Granger (1909) assigned the rocks that now comprise the Kinney Rim Member to the underlying Green River Formation. Roehler (1973) found that rocks stratigraphically below the "lower brown sandstone" (the base of Granger's Washakie Formation) were lithologically more similar to those of the overlying Washakie Formation than to the underlying Green River Formation. These rocks are bound below by the "persistent white ridge marker bed" (bed 515) and above by the unconformable persistent "lower brown sandstone" (bed 569), and thus constitute a mappable unit, named the Kinney Rim Member of the Washakie Formation. Granger (1909) did not recognize any rocks stratigraphically higher than those topping Haystack Mountain. Roehler (1973) and Turnbull (1972, 1978) independently recognized that rocks in the geographic center of the basin were stratigraphically higher than those of Haystack Mountain; this stratigraphically higher part of the section now constitutes the upper unit of the Adobe Town Member. The units of the Adobe Town Member were not formally divided by Roehler (1973) because they cannot be differentiated on the basis of persistent mappable beds.

Based on the mammalian fauna and lithologic changes, both Roehler (1973) and Turnbull (1978) placed the early–late Bridgerian boundary within the Kinney Rim Member (Roehler at ~bed 540; Turnbull at ~540–~559), the Bridgerian–Uintan boundary between the lower and middle units of the Adobe Town Member (bed 620; Granger's bed 11), and the early–late Uintan boundary between the middle and upper units of the Adobe Town Member (~bed 675). Of these boundaries, only one, the Bridgerian–Uintan boundary, was recognized by Granger (1909). Granger placed this boundary in the same place Roehler (1973) and Turnbull (1972) later did, between his beds 10 and 11 (bed 620 of Roehler, 1973), based on biostratigraphic distributions of Bridgerian and Uintan taxa. Roehler's (1973) placement of the early–late Bridgerian boundary and the early–late Uintan boundary was tentative and based on lithologic changes, not the biostratigraphic occurrence of diagnostic taxa. Two taxa, *Hyrachyus* near *H. modestus* and *Sciuravus* cf. *nitidus,* were used as tentative evidence for the placement of the early–late Bridgerian boundary in the Kinney Rim Member (Turnbull, 1972; Roehler, 1973). These taxa and their use as early Bridgerian indicators are discussed in more detail later.

The stratigraphic distributions within the Washakie Formation of the perissodactyl taxa reported here are shown in Table 5. When compared to the presently known temporal distributions of these taxa elsewhere (shown in Table 4), the following

TABLE 4. Currently recognized chronologic distributions of selected North American middle and late Eocene perissodactyl taxa.

Taxon	Bridgerian			Uintan			Duchesnean
	G	EB	LB	S	EU	LU	ED
*Isectolophus annectens**	–	–	–	–	X[1]	X[1]	–
Isectolophus latidens	–	X[1]	X[1]	–	–	–	–
Eomoropus amarorum	–	–	–	–	X[11]	–	–
Helaletes nanus	X[12]	X[1]	X[1]	–	–	–	–
Helaletes intermedius†*	–	–	X[1]	–	–	–	–
Dilophodon minusculus	–	–	X[1]	X[8,10]	–	–	–
*Dilophodon leotanus**	–	–	–	–	–	X[1]	–
*Colodon**	–	–	–	–	–	X[1]	X[1]
Forstercooperia grandis†	–	–	–	–	X[2]	–	–
Forstercooperia minuta	–	–	–	–	–	–	X[2]
Triplopus cubitalis	–	–	–	–	X[3]	–	–
Triplopus implicatus	–	–	–	–	X[3]	–	–
*Triplopus obliquidens**	–	–	–	–	X[3]	–	–
*Triplopus rhinocerinus**	–	–	–	–	–	X[3]	–
Amynodon advenus	–	–	–	X[8]	X[4]	X[4]	–
*Amynodon reedi**	–	–	–	–	X[4]	–	–
Hyrachyus modestus	X[5]	X[5]	X[5]	–	–	–	–
Hyrachyus eximius	–	–	X[5]	X[6]	–	–	–
*Epitriplopus uintensis**	–	–	–	–	–	X[3]	X[3]?
Orohippus	X[7]	X[7]	X[7]	–	–	–	–
Epihippus gracilis	–	–	–	–	X[10]	X[10]	–
Epihippus uintensis	–	–	–	X[10]	X[10]	X[10]	X[10]
Palaeosyops	X[12]	X[9]	X[9]?	–	–	–	–
Telmatherium	–	–	X[7]	–	–	–	–
Mesatirhinus	–	–	X[7]	–	–	–	–
Metarhinus	–	–	–	X[8]	X[7]	–	–
Dolichorhinus	–	–	–	–	X[7]	–	–

G, Gardnerbuttean; EB, early Bridgerian; LB, late Bridgerian; S, Shoshonian; EU, early Uintan; LU, late Uintan; ED, early Duchesnean.

1, Radinsky 1963; 2, Lucas et al. 1981; 3, Radinsky 1967a; 4, Wall 1982; 5, Radinsky 1967b; 6, Flynn 1983; 7, Krishtalka et al. 1987; 8, Flynn 1986; 9, Mader 1989; 10, MacFadden 1980; 11, Lucas and Schoch 1989; 12, Robinson 1966.

* Taxa not found in the Washakie Formation.

† Taxa previously reported from the Washakie Formation but not present in FMNH collections.

general conclusions can be made: 1) The Kinney Rim Member and the lower unit of the Adobe Town Member contain only taxa restricted to the late Bridgerian or that range broadly throughout the Bridgerian, indicating a late Bridgerian age for those units; 2) the middle unit of the Adobe Town Member contains taxa restricted to the earliest–early Uintan or that range broadly (e.g., Bridgerian–early Uintan or early–late Uintan), indicating an earliest–early Uintan age for all or most of the unit; and 3) the only perissodactyl from the upper unit of the Adobe Town Member is *Epihippus gracilis*, known to range from early to late Uintan. Below we discuss each member and unit within the formation and the biochronologic significance of each taxon known from it.

Kinney Rim Member

Turnbull (1972) reported finding *Hyrachyus* near *H. modestus* and *Sciuravus* cf. *nitidus* from the Kinney Rim Member. He used these taxa as indicators of an early Bridgerian age for the lower part of the Kinney Rim Member (Roehler, 1973; Turnbull, 1978). Both *H. modestus* and *S. nitidus* range throughout the Bridgerian (Krishtalka et al., 1987) and their presence does not necessarily indicate an early Bridgerian age. In addition, the specimen reported as *Hyrachyus* near *H. modestus* by Turnbull (1972) is PM 26128 and is here thought to be *H. eximius*, not *H. modestus* (see systematic section).

The Kinney Rim Member preserves *Mesati-*

TABLE 5. Stratigraphic distribution within the Washakie Formation of perissodactyl taxa reported here.

Taxon	Kinney Rim Member	Adobe Town Member		
		$Twka_1$	$Twka_2$	$Twka_3$
Orohippus sp.		X		
Epihippus gracilis				X
Telmatherium sp.		X		
Mesatirhinus sp.		X		
Metarhinus sp.			X	
Dolichorhinus sp.			X	
Isectolophus latidens		X		
Eomoropus amarorum			X	
Helaletes nanus	X			
Dilophodon minusculus			X	
Hyrachyus modestus	X	X		
Hyrachyus eximius	X	X		
Triplopus cubitalis			X	
Triplopus implicatus			X	
cf. *Forstercooperia minuta*			X	
Amynodon advenus			X	X

rhinus sp., *Helaletes nanus, Hyrachyus modestus,* and *Hyrachyus eximius. Helaletes nanus* ranges throughout the Bridgerian and *H. modestus* occurs throughout the Bridgerian. *Mesatirhinus* is currently restricted to the late Bridgerian (Mader, 1989). *Hyrachyus eximius* is currently known to have its first occurrence in the late Bridgerian (Radinsky, 1967b; Gazin, 1976; although Gazin reported a specimen of *H. eximius* from just below the Sage Creek White Layer in the Bridger Basin, this layer is the dividing line between the early and late Bridgerian in the Bridger Basin). The presence of *H. eximius* (PM 26128) near the base of the Kinney Rim Member (bed 527) indicates that early Bridgerian-aged rocks are probably not present within the Washakie Formation, and the early–late Bridgerian boundary in the Washakie Basin lies within the underlying Green River Formation.

At present, the first occurrence of *H. eximius* is confidently placed at the early–late Bridgerian boundary. The last occurrence of *H. eximius,* however, is uncertain. Flynn (1983) assigned an almost complete skull and right dentary from the Washakie B (AMNH 107978, a cast of UW 1937) to *H. eximius. Hyrachyus eximius* has not been recognized previously as occurring in the early Uintan. Upon examination of UW 1937 (FMNH 39232, also a cast of UW 1937), we agree that it is probably *Hyrachyus,* and not the taxon most similar to it, *Triplopus*; it is within the size range previously reported for *H. eximius* (Radinsky, 1967b). A range extension of *Hyrachyus,* represented by *H. eximius,* into the early Uintan would not affect the above reasons for not recognizing early Bridgerian-aged rocks within the Washakie Formation.

Adobe Town Member—Lower Unit

The lower unit of the Adobe Town Member historically has been considered late Bridgerian in age (Granger, 1909; Roehler, 1973; Turnbull, 1978). This has been based on the occurrence of characteristic late Bridgerian taxa within the unit (e.g., *Uintatherium, Mesatirhinus, Notharctus, Hyrachyus, Sinopa*). More recently, in a study combining biostratigraphy, magnetic polarity stratigraphy, and radioisotopic dating, Flynn (1986) proposed an earliest Uintan (Shoshonian Subage) age for some upper portion of the lower unit of the Adobe Town Member. Flynn (1986) based his proposal on the finding that the Bridgerian–Uintan boundary, and earliest Uintan (Shoshonian) faunas, occurred within magnetochron C20R in Eocene sediments of the East Fork Basin area of northwest Wyoming and the San Diego area of California. Within the Washakie Formation, a reversed polarity interval, correlated by Flynn (1986) to Chron C20R, is approximately equivalent to the lower unit of the Adobe Town Member; therefore, the Bridgerian–Uintan boundary should lie within the lower unit. Flynn (1986, pp. 379–380) defined the Bridgerian–Uintan boundary by the first occurrence of *Amynodon,* and characterized earliest Uintan faunas by the co-occurrence of small-bodied taxa previously known only from the late Bridgerian or older intervals with large-bodied

taxa previously known only from the early Uintan or younger intervals. The larger-bodied early Uintan taxa were predominantly, but not exclusively, perissodactyls.

At present, the following perissodactyl taxa have been recovered from the lower unit of the Adobe Town Member: *Orohippus* sp., *Telmatherium* sp., *Mesatirhinus* sp., *Isectolophus latidens, Hyrachyus modestus,* and *Hyrachyus eximius.* The defining Shoshonian (earliest Uintan) taxon, *Amynodon,* is not present. Each of these other taxa is well known from late Bridgerian deposits of western North America. Although some (*Hyrachyus*) may have earliest Uintan last occurrences, this is insufficient evidence for demonstrating an earliest Uintan (Shoshonian) age for the lower unit of the Adobe Town Member. This unit does contain characteristic "Bridgerian" taxa (*Hemiacodon gracilis, Microsyops annectens, Notharctus robustior, Hyopsodus paulus*) noted as occurring in the earliest Uintan by Flynn (1986); their presence alone, however, is also insufficient evidence for demonstrating an earliest Uintan age for the unit. At present, the known taxa from the lower unit of the Adobe Town Member indicate a late Bridgerian age, although a Shoshonian (earliest Uintan) age is still possible for part of the unit.

The absence of a definitive earliest Uintan fauna from the lower unit of the Adobe Town Member may be a taphonomic artifact. Many of the "Uintan" taxa used to define or characterize the earliest Uintan are larger in size (*Amynodon, Metarhinus, Achaenodon*). Unfortunately, the most fossiliferous beds known from the lower unit of the Adobe Town Member ("middle red beds" of Roehler, 1973) typically produce only smaller-bodied taxa (rodents, primates, insectivores). Preliminary analysis of the fossil material collected to date indicates that these beds represent paleosols—horizons where there is a bias (although not exclusive) toward the preservation of smaller skeletal elements, especially isolated teeth and jaws (Bown & Kraus, 1981; Bown & Beard, 1990). Thus, a preservational (and potential collection) bias against larger-bodied Uintan taxa may exist. Increasing our future collection efforts in more environmentally diverse beds in the lower unit of the Adobe Town Member may yield a greater diversity of larger-bodied taxa from the lower unit of the Adobe Town Member.

Adobe Town Member—Middle Unit

The middle unit of the Adobe Town Member historically has been considered early Uintan in age (Granger, 1909; Roehler, 1973; Turnbull, 1978). This has been based on the occurrence of characteristic early Uintan taxa (*Eobasileus, Achaenodon, Amynodon, Dolichorhinus, Metarhinus*) within the unit.

Perissodactyl taxonomic diversity and abundance are highest for the Washakie Formation in the middle unit of the Adobe Town Member. The taxa present are *Dolichorhinus* sp., *Metarhinus* sp., *Eomoropus amarorum, Dilophodon minusculus, Triplopus cubitalis, Triplopus implicatus,* cf. *Forstercooperia minuta,* and *Amynodon advenus. Dilophodon minusculus* has been thought to be restricted to the late Bridgerian (Radinsky, 1963). The remaining taxa listed above have earliest–early Uintan first occurrences (Flynn, 1986, Krishtalka et al., 1987). Thus, the middle unit of the Adobe Town Member is the only unit within the Washakie Formation where Bridgerian and Uintan taxa are documented to overlap in occurrence. This indicates an earliest Uintan age (Shoshonian Subage) for some lower portion of the middle unit of the Adobe Town Member.

Alternatively, the occurrence of *Dilophodon minusculus* in the middle unit of the Adobe Town Member could be interpreted as a range extension for that taxon to include the early Uintan. The occurrence of other nonperissodactyl taxa (*Hyopsodus* and *Notharctus robustior*) known to occur in the Bridgerian (but also in the earliest Uintan) also indicates a "Bridgerian" component to the fauna of the middle unit.

Adobe Town Member—Upper Unit

The upper unit of the Adobe Town Member was not included in Granger's Washakie Formation. This portion of the section was independently recognized by Roehler (1973) and Turnbull (1972, 1978) as being stratigraphically above the sediments capping Haystack Mountain (= top of Granger's [1909] section). Thus, the upper unit is younger than the beds capping Haystack Mountain, but by how much is still in question. Roehler (1973) speculatively assigned a late Uintan age to the upper unit based on lithologic changes he interpreted as a change in "sedimentary regime." Roehler (1973) reported no fossil mammal specimens from the upper unit. Turnbull (1978) also reported an inadequate fossil mammal record from the upper unit and simply reiterated Roehler's speculation of a late Uintan age.

Epihippus gracilis is the only perissodactyl known from the upper unit of the Adobe Town Member. The paucity of specimens makes place-

ment of the early–late Uintan boundary within the Adobe Town Member difficult. In addition, the known temporal span of *E. gracilis* is the entire Uintan, which prevents further biochronologic subdivision based on its presence within the unit. Additional recent collections of nonperissodactyl taxa from the upper unit indicate the absence of late Uintan taxa from the upper unit (McCarroll et al., 1993, in press), this fauna will be reported elsewhere (McCarroll, 1995, in prep.).

The currently recognized temporal distributions for selected middle and late Eocene perissodactyl species are shown in Table 4. Several taxa of late Bridgerian or early Uintan age have not been recognized yet from the Washakie Formation, even though the temporal span of the formation indicates they could have occurred here. *Palaeosyops* has been reported from the Washakie Formation (Osborn, 1929), but we have no specimens of *Palaeosyops* in the FMNH collections. *Helaletes intermedius* (= *Desmatotherium guyotii*) may in fact be known from the Washakie Formation, if the type of *D. guyotii* (YMP-PU 10166) is actually from the Washakie Basin rather than the Bridger Basin (see Radinsky, 1963, pp. 48–50). Radinsky (1963) commented on the rarity of *H. intermedius* in general. We have yet to find any specimens that we confidently assign to *H. intermedius,* presumably because of its rarity. *Amynodon reedi,* originally described from the Poway Conglomerate of San Diego, California (Stock, 1939), is now reported from early Uintan sediments of White River, Utah, and the Uinta Basin, Utah (Wall, 1982). It has not been documented in the Washakie Formation. *Triplopus obliquidens* and *Triplopus rhinocerinus* are both known from the Uinta Formation, but so far as we can tell they are absent in the Washakie Formation. This may be due in part to taxonomy; *T. obliquidens* of the Uinta Basin may be synonymous with *T. implicatus* of the Washakie Basin (see Radinsky, 1967a, p. 14).

Dilophodon leotanus, presently restricted to the late Uintan, is not identified here from the Washakie Formation, but is known from several late Uintan faunas from Utah, Wyoming, and Montana (Radinsky, 1963). Its absence is assumed to be due to the lack of late Uintan age sediments in the Washakie Formation. The lack of late Uintan age sediments may also explain the lack of *Colodon* (late Uintan–Whitneyan) from the Washakie Formation.

Ecological, paleogeographic, and climatic explanations could all be used to explain the absence of these taxa from the Washakie Formation. In addition, the Washakie Formation has long had the reputation for being relatively unfossiliferous, thus small sample size may also be a factor. Their presence in other geographically proximate basins and temporally equivalent formations, and the steadily growing collections from the Washakie Basin, would indicate to us that some causal mechanism might have prevented their entry into the Washakie Basin. Unfortunately, too little is known about the detailed paleogeographic and climatic conditions at the time to confidently speculate. Furthermore, the ecologic preference and interactions of the taxa involved are still uncertain, and the need for taxonomic revisions of some groups hinders direct basin-to-basin comparisons.

Conclusions

The following biochronologic conclusions can be drawn from the perissodactyls of the Washakie Formation and their biostratigraphic distributions.

1) Early Bridgerian taxa are not currently known from the Washakie Formation. The occurrence of *Hyrachyus eximius,* a late Bridgerian first occurrence taxon, from near the base of the Kinney Rim Member places the early–late Bridgerian boundary within the underlying Green River Formation.
2) The Kinney Rim Member and the lower unit of the Adobe Town Member both appear to be best assigned a late Bridgerian age.
3) Earliest Uintan (Shoshonian Subage) faunas may be known from the lower portion of the middle unit of the Adobe Town Member. The middle unit of the Adobe Town Member is the only unit in which larger-bodied taxa that occur in the early Uintan co-occur with smaller-bodied taxa that occur in the late Bridgerian, as is typical of the Shoshonian elsewhere. The upper portion of the middle unit of the Adobe Town Member is early Uintan in age.
4) Late Uintan taxa are currently unknown from the Washakie Formation. To date, no late Uintan first occurrence taxa are known from the upper unit of the Adobe Town Member.

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Appendix 1: Field Museum Localities Cited in Text

The following localities are cited in the text. Localities cited in the text but not listed here can be found in Turnbull (1978).

Twka$_1$ JJF 7-24-90-1 S½, SW¼, NE¼, Sec. 19, T16N, R97W
Twka$_1$ JJF 7-26-92-1 SW¼, Sec. 30, T16N, R97W
Twka$_1$ JJF 7-28-92-1 E½, Sec. 13, T13N, R96W & W½, Sec. 18, T13N, R95W
Twka$_1$ JJF 7-28-92-2 SE¼, NW¼ & NE¼, SW¼, Sec. 7, T13N, R95W
Twka$_1$ JJF 8-11-93-1 S½, NE¼ & N½, SE¼, Sec. 36, T16N, R98W
Twka$_1$ JJF 8-13-93-1 N½, NW¼, Sec. 6, T13N, R95W & S½, S½, Sec. 31, T14N, R95W
Twka$_2$ JJF 7-25-92-1 N½, NW¼, Sec. 2, T16N, R97W & SE¼, SE¼, Sec. 35, T17N, R97W
Twka$_2$ JJF 7-25-92-2 NE¼, SE¼, Sec. 36 & W½, NW¼, SW¼, Sec. 31, T17N, R97W
Twka$_3$ JJF 7-21-90-1 SW¼, NE¼, NE¼, Sec. 23, T14N, R98W

Appendix 2: *Metarhinus* sp. Specimens from the Monospecific Titanothere Quarry Reported by Turnbull and Martill (1988)

Specimens assigned here to *Metarhinus* from the monospecific titanothere quarry initially described by Turnbull and Martill (1988): These specimens were assigned to *Mesatirhinus* by Turnbull and Martill (1988), prior to Mader's (1985) revision of the Brontotheriidae. Using Mader's (1989) character sets, we amend the generic assignment to *Metarhinus*.

Skull and maxillary specimens: PM 28012, 28345, 28348, 30384–5, 30388, 30431–2, 35931–2, 36000, 36053–4, 36072, and 1 uncatalogued skull.

Dentaries: PM 28001–4, 28006–10, 28014, 28342–4, 28359A–D, 30422, 30434–5, 35928A–B, 35931, 35933, 35970, 35996, and 54422.

Isolated teeth: PM 28015, 28023, 28024–31, 28039, 28347, 28350–3, 28358, 28360, 28363–4, 30393–4, 30396–400, 30413, 30417, 35938–40, 35943–51, 35953–9, 35964–8, 35971–3, 35975, 35979–81, 35998, 36004–5, 36007, 36012–4, 36016, and 36055–71.

Postcranial specimens: PM 28005, 28008–9, 28013, 28037–8, 28346, 28348–9, 28354–65, 30383–7, 30389–92, 30395, 30401–16, 30418–21, 30423–30, 30433, 35924, 35928–30, 35935, 35941–2, 35952, 35960–3, 35974, 35976, 35978, 35982–6, 35989–91, 35993–5, 35997, 35999, 36001–3, 36006–11, 36015, 36023, and 36046–52.

The 27 jaw specimens (MNI = 25) listed in Turnbull and Martill (1988, Table II) allowed for age estimates ranging from about 3 months to well over 15 years, with both sexes represented. One dentary not included in Turnbull and Martill (1988, Table II) has since turned up, which accounts for the change in numbers.

A Selected Listing of Other *Fieldiana: Geology* Titles Available

A Preliminary Survey of Fossil Leaves and Well-Preserved Reproductive Structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota. By Peter R. Crane, Steven R. Manchester, and David L. Dilcher. *Fieldiana: Geology,* n.s., no. 20, 1990. 63 pages, 36 illus.

Publication 1418, $13.00

Protoptychus hatcheri Scott, 1895. The Mammalian Faunas of the Washakie Formation, Eocene Age, of Southern Wyoming. Part II. The Adobetown Member, Middle Division (= Washakie B), Twka/2 (in Part). By William D. Turnbull. *Fieldiana: Geology,* n.s., no. 21, 1991. 33 pages, 12 illus.

Publication 1421, $13.00

A Catalogue of Type Specimens of Fossil Vertebrates in the Field Museum of Natural History. Classes Amphibia, Reptilia, Aves, and Ichnites. By John Clay Bruner. *Fieldiana: Geology,* n.s., no. 22, 1991. 51 pages, 1 illus.

Publication 1430, $15.00

The Ear Region in Xenarthrans (= Edentata: Mammalia). Part II. Pilosa (Sloths, Anteaters), Palaeanodonts, and a Miscellany. By Bryan Patterson, Walter Segall, William D. Turnbull, and Timothy J. Gaudin. *Fieldiana: Geology,* n.s., no. 24, 1992. 79 pages, 24 illus.

Publication 1438, $20.00

Comparative Microscopic Dental Anatomy in the Petalodontida (Chondrichthyes, Elasmobranchii). By Rainer Zangerl, H. Frank Winter, and Michael C. Hansen. *Fieldiana: Geology,* n.s., no. 26, 1993. 43 pages, 35 illus.

Publication 1445, $16.00

Status of the Pachypleurosauroid *Psilotrachelosaurus toeplitschi* Nopcsa (Reptilia, Sauropterygia), from the Middle Triassic of Austria. By Olivier Rieppel. *Fieldiana: Geology,* n.s., no. 27, 1993. 17 pages, 9 illus.

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Osteology of *Simosaurus gaillardoti* and the Relationships of Stem-Group Sauropterygia. By Olivier Rieppel. *Fieldiana: Geology,* n.s., no. 28, 1994. 85 pages, 71 illus..

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